

Feeding by fish visiting inundated subtropical saltmarsh

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Abstract

Australian saltmarshes are inundated less frequently and for shorter periods than most northern hemisphere marshes, and when inundated provide transient fish a diverse prey assemblage. We determined the extent of feeding on saltmarsh by examining stomach contents of a common marsh transient, glassfish (*Ambassis jacksoniensis*), in the Coombabah estuary in subtropical Queensland. We tested the hypotheses that fish caught after visiting the marsh (after (M)) would have similar quantities of food (stomach fullness index, SFI) but different prey composition (abundance, weight) both to fish collected before (Before) saltmarsh inundation and to fish that had not visited the marsh but were caught after marsh inundation (After (NM)). Sampling was done on multiple nights over 3 months in winter, when the marsh is inundated on spring tides at night only. SFI values of After (M) fish were significantly higher (SFI \approx 12%) than those of Before and After (NM) fish (SFI \approx 0–1%). After (M) fish also had very different prey composition, eating more crab zoea (>100 zoea fish⁻¹) than Before fish (10) and After (NM) fish (0). After (M) fish showed a consistent pattern in zoea abundances among sampling nights, in all months, with lower zoea abundances on the first night that the marsh was inundated than on subsequent nights. This is attributed to the synchronized spawning of crabs resident on the marsh, releasing their zoea on the ebb of the second inundating tide of the month. Fish stomach contents did not differ before and after smaller high tides not inundating the marsh (SFI \approx 0–1%). Experimental evidence showed that glassfish evacuate their stomach contents in about an hour under starvation conditions, further strengthening our contention that the stomach contents of After (M) fish represent prey ingested on the marsh. The demonstration of intensive feeding by fish visiting this marsh points to a potentially important role of saltmarsh in the trophodynamics of subtropical Australian estuaries.

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1. Introduction

Saltmarsh habitat has long been considered to have importance beyond its boundaries. Broad-scale correlations between the area of saltmarsh in estuaries and the harvested weight of fisheries species (Boesch and

Turner, 1984) gave rise to the concept that saltmarsh is important in the nutrition of fish. On saltmarshes along the east coast of North America, small fish that remain on the marsh during the entire tidal cycle feed on marine invertebrates (Kneib and Stiven, 1978) and insects (Moy and Levin, 1991). These resident fish are themselves predated upon by larger fish visiting the marsh edge at high tide (Kneib, 1997). They form part of a series of predator–prey relationships known as trophic relay, that describes a net movement of biomass and

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energy from saltmarsh to deeper estuarine and coastal waters (Kneib, 2000).

Several studies have demonstrated feeding on saltmarsh by comparing stomach fullness and prey composition of fish entering and leaving marsh habitat. Studies in the USA (Archambault and Feller, 1991; Rountree and Able, 1992; Nemerson and Able, 2004; and in brackish marshes, Rozas and LaSalle, 1990) and Europe (Lefevre et al., 1999; Laffaille et al., 2001, 2002) have detected higher stomach fullness after fish visit marshes. These studies have recorded a range of prey types, dominated by marine invertebrates (e.g. polychaete worms, amphipods) with occasional terrestrial (insect) invertebrates. Australian marshes are higher in the intertidal than most of the northern hemisphere marshes studied, and are therefore inundated less frequently and for shorter periods (Connolly, 1999). The feeding behaviour of fish on Australian saltmarshes should not therefore be assumed to be the same as on the better studied marshes of the northern hemisphere.

The extensive subtropical saltmarshes of eastern Australia are visited by large numbers of small fish when inundated (Thomas and Connolly, 2001). Morton et al. (1987) described the feeding behaviour of fish caught in a small creek draining one of these marshes. The marine component of the diet of the six species examined was dominated by benthic invertebrates, predominantly adult shore crabs, although some species also ate planktonic invertebrates (crab larvae and amphipods). The diets also included a range of terrestrial invertebrates, especially a striking diversity of adult insects from eight different orders. It cannot be assumed, however, that the diets described by Morton et al. (1987) are the result of feeding behaviour on the marsh itself (Connolly et al., 1997), since it has been shown elsewhere that fish can remain in marsh creeks and feed without entering the inundated marsh (Szedlmayer and Able, 1993; Le Quesne, 2000). Some marshes in subtropical Australian waters have brackish, semi-permanent pools high on the marsh. Fish occurring in these pools feed predominantly on insect larvae that breed there (Morton et al., 1988). Other reports on fish feeding on Australian marshes are from temperate waters in southern Australia. Fish moving over the edge of narrow marshes in Victoria feed on amphipods and hemipteran insects (Crinall and Hindell, 2004). On a marsh in New South Wales, the same species of fish as in the current study, *Ambassis jacksoniensis* (Macleay), was found to feed on shore crab larvae and insects (Mazumder et al., 2006).

The role of saltmarsh in fish feeding in subtropical Australian waters is not yet understood, but the need to

know is made all the more important by the substantial losses of this habitat over the past 50 years. Saltmarsh along the east coast of Australia has been one of the habitats most poorly protected from urban and agricultural development (Adam, 2002). Human activities such as reclamation, pollution, altered drainage regimes and the destruction of vegetation by off-road vehicles have affected marshes directly (Connolly and Bass, 1996; Breiffuss and Connolly, 2004). Saltmarshes have also declined in area because of mangrove incursion due to rising sea-levels (Saintilan and Williams, 1999). Areal losses in the order of 50% have been recorded in the subtropical waters of southern Queensland (Hyland and Butler, 1989).

Models of fish feeding behaviour on marshes rely on comparisons of stomach contents before and after fish visit marshes. Two additional comparisons are required to provide compelling evidence for the importance of feeding in marsh habitat, especially where marshes are inundated only infrequently. First, a check is required that whatever differences occur in stomach content before and after fish visit inundated marshes do not also occur on high tides that do not inundate marshes. This check was made by Laffaille et al. (2001) during their study of the feeding of sea bass (*Dicentrarchus labrax*) in France. Second, a full demonstration of the importance of inundated marsh habitat requires examination of stomachs of fish not visiting the marsh but caught at the same time as fish leaving the marsh.

Our model is that the infrequent inundation of saltmarshes in Australia means that: a) prey productivity on the marsh is lower than in other intertidal habitats, but because fish only rarely gain access, prey availability will be about the same as in other habitats, and b) terrestrial animals are relatively abundant and form a greater part of the diet of fish on marshes than in other estuarine habitats. Fish would feed in the estuary prior to the marsh being inundated, and continue feeding on the marsh once inundated. We hypothesise that fish leaving a marsh will have similar stomach fullness to before, but different prey composition, biased towards terrestrial sources. We also hypothesise that fish that have not entered the marsh, but are caught at the same time as fish departing the marsh, will have the same stomach fullness and composition as before the marsh was inundated. Fish sampled before and after high tides that are too low to inundate the marsh will not show differences in stomach contents since a high tide in itself is not important in our model. We tested the hypotheses using an abundant estuarine fish, *A. jacksoniensis*, on a saltmarsh in southern Queensland, Australia.

2. Materials and methods

2.1. Study site

The study was done on the western shore of Coombabah Lake, a large, shallow (0–3 m deep) lake in the estuarine section of Coombabah Creek. The creek provides fresh water from a partly urbanised catchment and also links the lake to the marine waters of the most southerly part of Moreton Bay, known as the Broadwater (Fig. 1). Rainfall occurs predominantly in a summer wet season in southern Queensland, and although salinity in the lake drops to less than 5 psu after heavy rainfall in the catchment, at the time of the study during the winter dry season, salinity was 28–33 psu. Parts of the lake are fringed by mangrove forests (dominated by *Avicennia marina*) backed by saltmarsh, but the shoreline at the site on the western side has little forest and the saltmarsh occurs immediately adjacent to extensive intertidal mudflats. The saltmarsh is dominated by saltmarsh grass (*Sporobolus virginicus*) with smaller patches of the succulents *Sarcocornia quinqueflora* and *Suaeda australis*.

Saltmarsh at the site is flooded at tidal amplitudes greater than 2.48 m (Brisbane River bar height), which occur only on spring tides, covering about 15% of the year. The marsh is flooded when lake waters breach the slight rise separating the marsh from mudflats, lasting about 2 h. The semi-diurnal tides in southern Queensland peak at night in winter and during the day in summer. During the current study, therefore, all flooding tides were at night, with high tides between 20.00 and 24.00 h, and all sampling occurred in this period.

2.2. Fish sampling

We studied the Port Jackson glassfish (*A. jacksoniensis*) because it was the most common species (>50% of the catch) in trial collections in early winter. Along with the congeneric, *A. marianus*, it dominates catches from subtropical saltmarsh in Australia (Thomas and Connolly, 2001; Mazumder et al., 2005). It occurs in about the same numbers far onto marshes (approximately 100 m) as near the marsh edge (Connolly, 2005). *A. jacksoniensis* has previously been shown to feed on crustaceans and other invertebrates (Mazumder et al.,

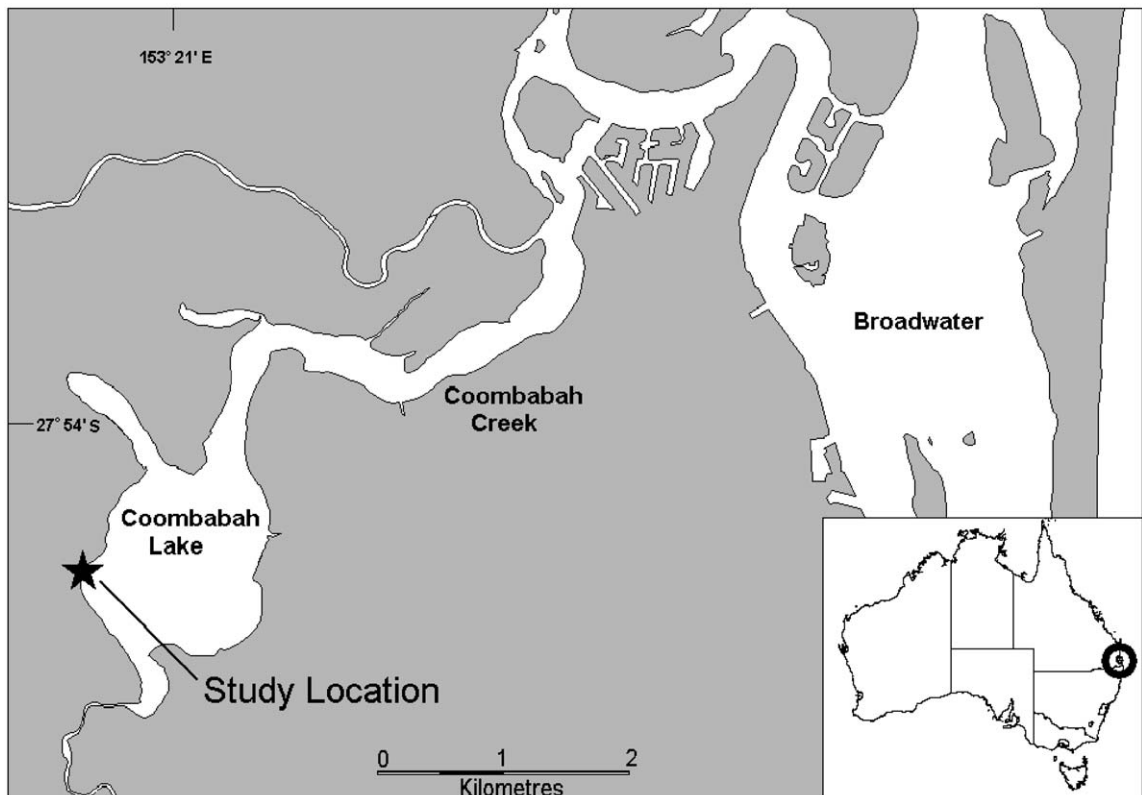


Fig. 1. Map of study location at Coombabah Lake, southeast Queensland, Australia.

2006), making it amenable to numerical analysis of stomach contents (Berg, 1979).

Glassfish were collected over the 3 months of the austral winter in 2004. Collections occurred over three consecutive spring tides at night in June and July, and on two nights in August (when the marsh was not inundated on the third night). The main comparison involved collecting glassfish under three treatments: 1) before entering the saltmarsh (Before), 2) after visiting inundated saltmarsh (After (M)), and 3) non-marsh fish collected after marsh inundation (After (NM)). Fish for the Before treatment were collected using fine-mesh seine nets on mudflats immediately adjacent to the marsh, between 0 and 60 min prior to marsh inundation. Fish for the After (M) treatment were caught using a technique similar to Laffaille et al. (1999), consisting of multi-chambered fyke nets set just onto the marsh with wings of 1 mm mesh set at 45° and facing the marsh interior. After (M) collections began when the tide began to ebb and ceased when the marsh was no longer inundated. Fish were removed from the back of the fyke nets and sacrificed as they were caught, to prevent feeding or digestion after capture. The positioning of the fyke nets meant that fish were directed into the nets as they departed the marsh interior, and made it impossible for fish to enter the net without having first spent time on the marsh. Fish for the After (NM) treatment were collected using fine-mesh seine nets over mudflats about 100 m seaward of the marsh edge, immediately that the tide began to ebb. The location and timing of this sampling maximised the chance of collecting glassfish that had not visited the marsh during that inundation event.

To ensure that the comparison of before and after marsh inundation reflected diets of fish on the marsh and not just on high tides generally, glassfish were also collected before and after non-spring high tides that inundated adjacent mudflats but not the marsh itself. These collections were done one week before and one week after the August period of spring tide marsh sampling, for two nights in each period. Fish were collected 1 hr before and 1 hr after the high tide at night.

Glassfish were collected at several points along a 200 m section of the shoreline of the lake, but collections for a particular treatment on a particular night were pooled to provide a large enough sample, and no analysis of spatial variability along the shore was attempted.

2.3. Stomach content analysis

Glassfish ranged in length from 28 to 53 mm (caudal fork length), with a unimodal distribution.

Lengths did not differ between treatments or months (ANOVA: both factors and interaction non-significant). Most fish were toward the middle of the size range, and we restricted our analysis to this common size class (30–45 mm), since too few small or large fish were collected to be able to differentiate any ontogenetic dietary differences from patterns among treatments. For the fish analysed, we tested and found no relationship between fish length and stomach fullness (Regression: $R^2=0.01$, $p=0.352$).

Diet was examined for 766 glassfish over the 3 months. Only stomach contents were analysed, because food items from the stomach are more intact and recognisable and are a more reliable guide to the diet just prior to capture than items from the posterior section of the digestive tract. Stomach contents also show less bias due to differential passage rates or digestion rates of different prey types (Berg, 1979). Stomach contents were identified to the lowest possible taxon, enumerated, and their size estimated (see below).

2.3.1. Stomach fullness

We used a reliable, repeatable measure of stomach fullness suitable for small, carnivorous fish. The stomach fullness index (SFI) was calculated for each fish as: AFDW contents (mg)/DW fish (g), where AFDW is the estimated ash-free dry weight of ingested prey and DW is the dry weight of the fish (Edgar, 1990; Connolly, 1995). AFDW was calculated by adding the AFDW estimates for all prey types identified in an individual fish (see below). Dry weights of fish were estimated from a length-dry weight regression calculated on a sample of 20 whole fish covering the range of sizes used in the study (Regression on log transformed weights: $R^2=0.91$, $p<0.001$).

2.3.2. Prey composition

Stomach composition was measured using three aspects of prey importance: 1) frequency of occurrence, 2) numerical abundances, and 3) weights (AFDW). Frequency of occurrence was calculated as the percentage of fish in a sample having a particular prey type in their stomach. Numerical prey abundances were determined by identification and enumeration of individual prey items using 100× magnification.

Estimates of the AFDW of prey at the time of ingestion were made using Edgar's (1990) method. This method is able to estimate weights of very small prey types, and avoids the pitfall of weighing prey in different states of digestion. Only digestible tissue is weighed; indigestible, hard body parts are excluded. After each individual prey item was identified, it was assigned with

the aid of a graticule to a mesh size category (6 categories between 2.00 and 0.75 mm) relating to the range of lengths of that taxon retained on different mesh sizes. These size ranges were determined from previously measured lengths of numerous specimens of each prey taxon (see Connolly, 1995). The AFDW of invertebrates can be related to sieve mesh size using Edgar's (1990) equation, $\log B = a + b \log S$, where B = AFDW (mg), S = sieve size (mm) and a and b vary depending on broad taxonomic category. Since each mesh size retains animals ranging from that mesh size to the next, S is expressed as a geometric mean calculated using the equation, $\log S = (\log S_i + \log S_{i+1})/2$, in which S_i = size of the i th mesh and S_{i+1} = size of the next mesh size up (Edgar, 1990). Most prey items in stomach contents were intact, but where occasional broken pieces were encountered, the size of prey was estimated from the body parts present, using the size of heads or eye spots as a guide. Different body parts judged to be part of the same animal were pooled to avoid overestimating abundance.

2.4. Data analysis

The main comparison among treatments for the three variables able to be analysed statistically (SFI, prey abundances and weights) was tested using an ANOVA with two factors: inundation treatment (Before, After (M), After (NM)) and month (June, July, August). It became obvious in the laboratory that the contents of fish in the After (M) treatment varied among nights within a month. We therefore ran an additional two-factor ANOVA on After (M) data separately, with the factors: night (night 1, 2, 3) and month (June, July). Data from August were initially excluded since only two nights could be sampled and the design would not have been orthogonal. However, we found that nights 2 and 3 were not significantly different for any variable in either June or July. We were therefore able to run a further analysis pooling those nights and including August data, with the factor night having just two levels (night 1, nights 2/3 pooled).

Analysis of prey importance based on weight (AFDW) tended to reduce the importance of very small prey types such as gastropod larvae and harpacticoid and calanoid copepods. Conversely, larger prey items, in particular insects, were more prominent. The patterns in weights among treatments were, nevertheless, the same for all taxa as those based on abundances. All ANOVA analyses for zoea weights showed the same patterns as for abundances, and results are not reported here in detail.

Analysis of stomach contents of fish collected on high tides that did not inundate the saltmarsh (non-spring tides) were analysed using an ANOVA with three factors: period (pre-spring tide, post-spring tide), night (night 1, 2), and inundation treatment (Before and After high tide).

2.5. Stomach evacuation rate

Information about stomach evacuation rates of fish helps in the interpretation of stomach content results in cases such as the present study where the period over which contents have been ingested is critical. Evacuation rates of small fish vary with temperature (Marnane and Bellwood, 1997; Boyce et al., 2000), and evacuation rates have not been measured for estuarine fish in subtropical waters. We measured the stomach evacuation rate of glassfish twice, once in each of the first two sampling periods, at the same time as the main fish collections. In each run of the experiments, 35 glassfish were collected from the survey sites. Five fish were sacrificed immediately, and the others were placed into an insulated tub of estuarine water. The water temperature was kept as similar as possible to that in the ambient estuarine water (Trial 1: mean 16 °C; Trial 2: 18 °C). Digestive processes also depend on the quantity and quality of food ingested (Johnston and Mathias, 1996). In particular, many animals can retain food for longer if feeding ceases (Logan et al., 2002). We therefore chose to measure the minimum evacuation rate (maximum retention time of food in stomach), by preventing fish from feeding once the experiments were underway. To achieve this we filtered (53 µm) the water to remove potential food. Five haphazardly selected fish from the tub were sacrificed each 20 min, until the last fish were killed after 120 min. The SFI of each fish was estimated as described above. Stomach fullness showed

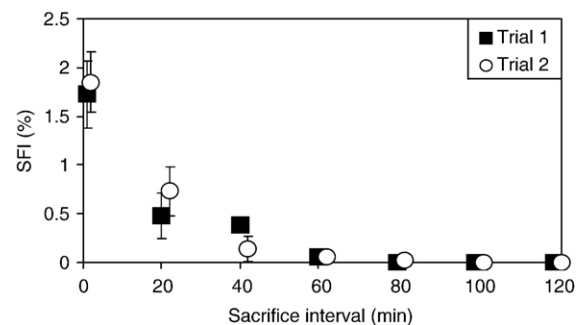


Fig. 2. Declining stomach fullness indices (SFI) of glassfish under starvation, for two trials (mean, SE; 5 fish sacrificed at each time in each trial).

an exponential decline in both trials. Nearly all food had been evacuated from stomachs after 1 h and by 100 min all fish had empty stomachs (Fig. 2).

3. Results

3.1. Stomach fullness

Up to 10% of fish in the After (M) treatment had empty stomachs, and the majority of fish in treatments Before (M) and After (NM) had empty stomachs (Fig. 3). SFI values did not vary significantly among months ($F_{2, 418}=0.2, p=0.809$), nor was there an interaction between months and inundation treatment ($F_{4, 418}=0.1, p=0.946$). However, SFI did differ among inundation treatments ($F_{2, 418}=13.3, p<0.001$; Fig. 3), with a Tukey test showing greater SFI values in After (M) than Before or After (NM).

Analysing differences in SFI among nights for After (M) data only, we found that SFI values did not differ among months ($F_{1, 265}=1.3, p=0.263$) nor was there an interaction between month and night ($F_{2, 265}=1.7, p=0.263$). The most obvious pattern was that SFI values varied among nights ($F_{2, 265}=.8, p<0.001$). Night 1 had significantly lower SFI values than nights 2 and 3, either pooled or separately.

We compared SFI values of fish collected before and after non-spring high tides that did not inundate the marsh to test whether the apparent greater consumption of prey indicated by the higher SFI values in the After (M) treatment might have resulted from a simple effect of feeding at high tide. The SFI values were similar before and after the high tide, and at both sampling periods pre and post the August

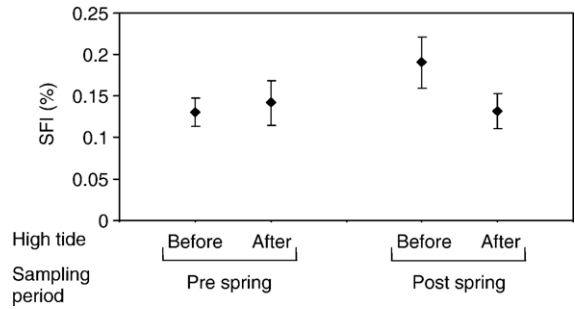


Fig. 4. SFI values of fish sampled before and after high tides, both prior to (pre) and after (post) the August inundating spring tide period, with nights combined (excluding fish with empty stomachs).

spring tide period (Fig. 4). None of the main factors or interaction terms in the three-factor ANOVA was significant (all $p>0.05$). The SFI values were $<1\%$, which was similar to values for the Before and After (NM) treatments in the spring tide August period.

3.2. Prey composition

The diet of glassfish consisted exclusively of invertebrates, with fifteen taxa identified (Table 1). Planktonic microcrustaceans and crab larvae were prominent, along with a range of adult (5 orders) and larval insects.

Table 1

Frequency of occurrence of prey items ingested by glassfish over all sampling periods, sampled before (Before) and after (After (M)) marsh inundation, and non-marsh fish after inundation (After (NM))

Prey item	Before <i>n</i> =366	After (M) <i>n</i> =400	After (NM) <i>n</i> =24
Crustacea			
Decapoda			
Brachyura			
Zoea	3.6	87.3	16.7
Megalopae	3.8	0.6	12.5
Mysidaceae	0.3		
Ostracoda	0.6		
Copepoda			
Calanoida	3.1	23.2	4.2
Harpacticoida	1.8		
Insecta			
Diptera adult		1.3	
Culicoid larvae		7.4	
Hymenoptera	0.6	1.8	
Hemiptera	0.6	1.8	
Odonata		0.3	
Coleoptera			
Dytiscidae	0.3	3.5	
Gastropoda			
Gastropod adult		0.3	
Gastropod larvae	2.5	11.4	
Polychaeta		0.3	

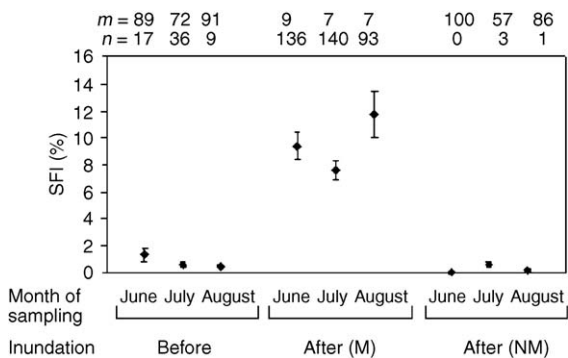


Fig. 3. Stomach fullness indices (SFI) of glassfish sampled before inundation and after inundation (After (M) and After (NM)) during June, July and August (mean, SE, excluding fish with empty stomachs). *m* = number of fish with empty stomachs (as % of total number of fish), *n* = number of fish after excluding empty fish.

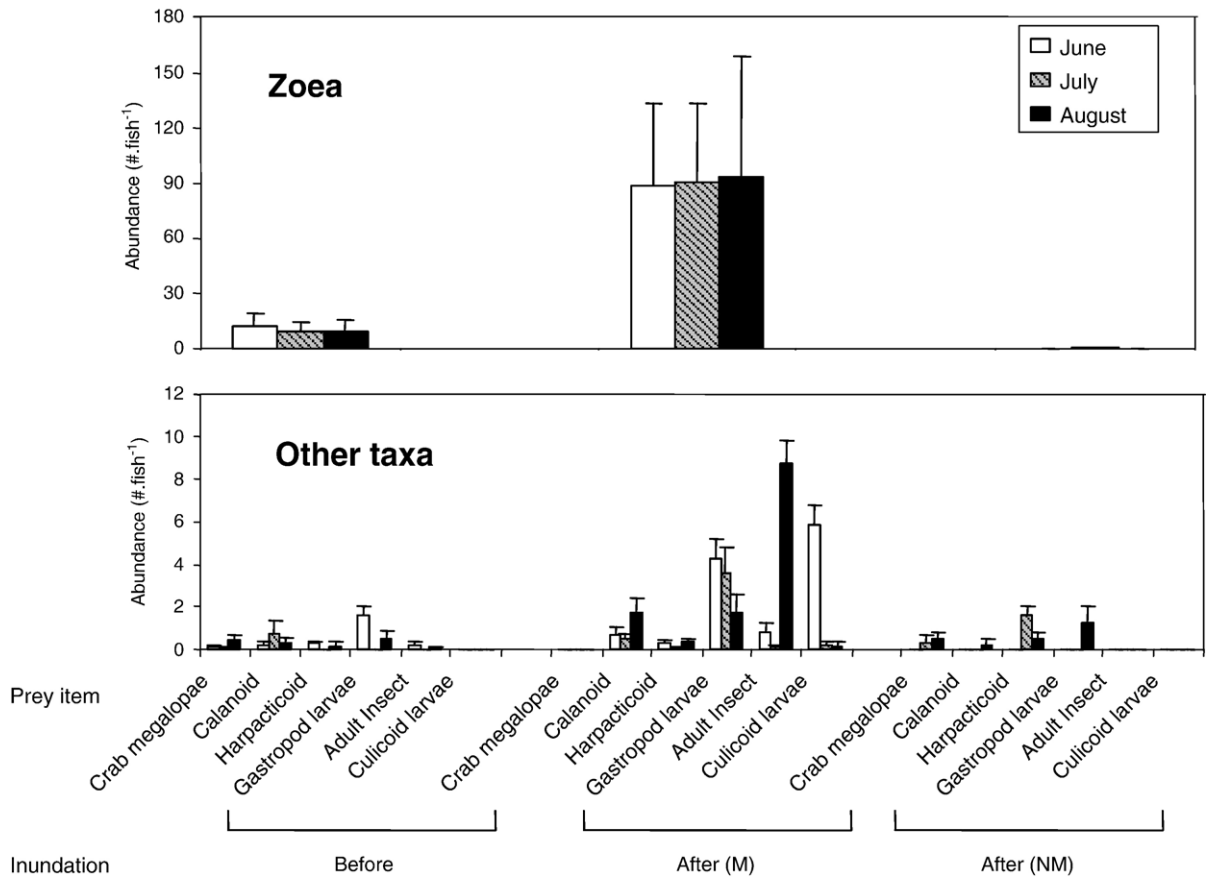


Fig. 5. Numerical abundances of crab zoea and other taxa in glassfish stomachs before inundation and after inundation (After (M) and After (NM)), for June, July and August (mean, SE, excluding fish with empty stomachs). Uncommon prey taxa not shown. Sample sizes: Before: June, July, August = 17, 36, 9, respectively. After (M): 136, 140, 93. After (NM): 0, 3, 1.

Fish in the Before and After (M) treatments had a wider range of taxa than those in the After (NM) treatment. Nearly all taxa occurred more frequently in fish sampled after being on the saltmarsh. Crab megalopae, however, occurred more frequently in Before and After (NM) treatments than After (M), and mysids and ostracods were found only in fish from Before inundation (Table 1). Crab zoea were the dominant prey for After (M) fish, and were found in over 87% of individual fish.

Crab zoea were clearly the most abundant prey in the After (M) treatment, with each fish containing on average about a hundred zoea (Fig. 5). Zoea was the only taxon that occurred frequently enough to allow statistical analysis. Even zoea occurred in very few fish in After (NM), so this inundation treatment was excluded from the ANOVA. There was no interaction between month and inundation for crab zoea abundance ($F_{2, 421}=0.5, p=0.699$), nor any difference among months ($F_{2, 421}=2.8, p=0.064$). Zoea abundances were,

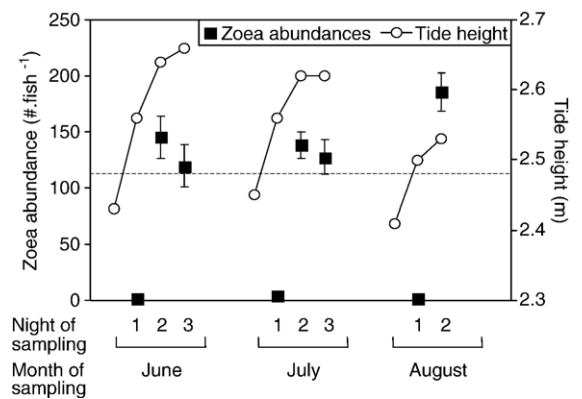


Fig. 6. Crab zoea abundances in glassfish feeding on marsh (After (M)), showing each night separately for each month (means, SE, scale on LHS). Tidal height is shown for each night of sampling and the night before sampling. Tidal height at which marsh is inundated (2.48 m) is shown by dotted line.

however, significantly higher in After (M) than Before samples ($F_{1, 421} = 58.6, p < 0.001$).

The analysis of variation among nights in zoea abundances in the After (M) treatment showed the same pattern as SFI values, above. The most obvious effect was that night 1 abundances were lower than in nights 2 and 3 ($F_{1, 339} = 286.9, p < 0.001$). The pattern of no or few zoea on the first night of sampling, but one to two hundred zoea per fish on subsequent nights, was consistent over the 3 months (Fig. 6). The first night of sampling in each month was also the first night on which the marsh was inundated (tidal amplitude > 2.48 m) during that month (Fig. 6).

Other prey categories were eaten in relatively small numbers (Fig. 5). Most prey types had higher abundances in the After (M) treatment, but crab megalopae showed a different pattern, being less abundant in the After (M) than in other treatments.

4. Discussion

This study provides compelling evidence that glassfish feed while on the saltmarsh at Coombabah Lake. This evidence comes from two comparisons. First, during periods of spring tides when the marsh was inundated at high tide, glassfish had empty or near-empty stomachs before they visited the marsh and much fuller stomachs after visiting the marsh. Glassfish caught within the estuary well away from the marsh, but at the same time as the post inundation collections, also had empty or near-empty stomachs. Second, on smaller, non-spring tides when the marsh was not inundated, there was no difference in stomach fullness between collections before and after high tide. On these smaller tides, glassfish had near-empty stomachs, with low stomach fullness indices similar to those of fish caught before entering the marsh in spring tide periods. The feeding pattern shown for killifish (*Fundulus heteroclitus*) in eastern USA (Weisberg et al., 1981), where feeding takes place at high tide regardless of whether the marsh is inundated, cannot be ascribed to glassfish. We believe that the suite of treatments and comparisons provides the most comprehensive evidence for specialist feeding on infrequently inundated marshes.

The concurrent sampling of fish away from the marsh with fish leaving the marsh was an important feature of our survey design. While it can be difficult to demonstrate that fish caught away from the marsh have not recently visited the marsh, in our study those fish had not been feeding prior to being caught, and this differentiated them from individuals collected from the marsh.

Although our second hypothesis, that the composition of glassfish diets differed for individuals visiting the marsh, was correct, our first hypothesis was not. We had expected fish to be feeding continuously as the tide inundated the unvegetated mudflats, and to then continue feeding upon the marsh. This would have resulted in similar stomach fullness indices before and after inundation. Yet fish caught prior to entering the marsh had empty or near empty stomachs. An increase in stomach fullness of fish after inundation has been shown previously in the USA (Rozas and LaSalle, 1990) and Europe (Laffaille et al., 2001, 2002), albeit on marshes inundated more frequently than those in Australia. The pattern of increased stomach fullness after visiting tidal marshes seems therefore to have some generality. Given that fish were found to have eaten little elsewhere in the estuary at high tide, and on smaller, non-inundating tides, the question arises as to how important this substantial feeding activity on the marsh is for the survival and growth of glassfish in the estuary. The marsh at Coombabah Lake is inundated only for one spring period each month during winter. Small fish such as these are unlikely to be able to survive the month between inundation periods without feeding (Wootton, 1998). It is possible that glassfish feed mainly during the day, but at night make use of the high food availability on the infrequently inundated marsh. Further work is needed, giving consideration to diel and seasonal differences (e.g. see Mazumder et al., 2006).

The predation of crab zoea by glassfish on the inundated marsh links the high intertidal habitat and the rest of the estuary. Zoea evidently become available each spring tide period only on the night after the marsh is first inundated, since this pattern occurred very clearly over all 3 months of sampling. The release of crab zoea on an ebb tide at night has previously been described from temperate saltmarshes (Hovel and Morgan, 1997; Mazumder et al., 2006) and tropical mangrove systems, including for the grapsid crab family that dominates the marsh at Coombabah Lake (Dittel and Epifanio, 1990). The release of larvae at night has been considered a strategy that has evolved because of predation by visual predators (Hovel and Morgan, 1997). At Coombabah, the most likely scenario is that the first inundating tide within a monthly cycle triggers crabs to release larvae the following night (Mazumder, 2004). Glassfish visit the marsh each night that they can, but it is only on the nights after the first inundating tide that zoea are available. The higher abundance of crab megalopae in fish that had not visited the marsh suggests that once larvae develop and spend more time in the water column, they become more widely distributed in the

estuary and are potential prey for fish at any state of the tide. Given the known seasonality of crab larval abundance (Dittel and Epifanio, 1990), further work is warranted in the Coombabah estuary on glassfish diets at seasons other than winter.

The nature of the trophic link between high intertidal habitats and deeper estuarine waters has been a topic of intensive research, with a recent emphasis on trophic relay (Kneib, 2000). The trophic relay model was developed in systems where the marsh is inundated every day and small fish spend much of their time on the marsh itself. Nevertheless, the spectacular consumption of crab larvae on the Coombabah marsh leads to the possibility that glassfish might act as a step in the transfer of marsh material to other parts of the estuary. Further study of predation on *A. jacksoniensis* is required. It is also possible that the biomass of crab larvae moving off the marsh is more important than the fraction consumed by glassfish.

All crab zoea were at first larval stage, which in grapsid crabs are released from adult females directly into the water column (Hovel and Morgan, 1997). Zoea were of a similar size ($\approx 500 \mu\text{m}$ long) in all treatments and periods. This size is typical of grapsid zoea (Cuesta et al., 2001). Zoea could not be identified to species given the difficulties in identification of zoeal stages within this family (Flores et al., 2003). However, one of the two most abundant shore crabs at Coombabah Lake, *Helograpsus haswellianus*, reproduces in winter (Green and Anderson, 1973), and it is very likely that the larvae were of this species (and see Mazumder, 2004).

Given the prominence of terrestrial animals, especially insects, in previous studies in subtropical Australia of fish diets adjacent to marsh (Morton et al., 1987) or in semi-permanent pools on the marsh (Morton et al., 1988), the dietary importance of crab larvae relative to insects is greater than expected. A relatively minor presence of terrestrial invertebrates in marsh fish diets has also been demonstrated elsewhere (Rozas and LaSalle, 1990; Laffaille et al., 2001). In the most comprehensive study of marsh fish diets on the east coast USA, annelid worms (oligochaetes and polychaetes) also occurred frequently in diets (Nemerson and Able, 2004). Of annelid worms, only polychaetes were recorded in glassfish diets at Coombabah Lake, and then only very occasionally and in tiny numbers. The lack of oligochaetes is probably a result of the greater salinity in the Coombabah estuary than at most sites surveyed by Nemerson and Able (2004). The very small contribution of polychaetes is surprising, however, since they are known to be preferred by other

night-feeding fish (Brewer and Warburton, 1992). Small fishes of southern Queensland estuaries have also been shown to consume large numbers of meiofaunal invertebrates in intertidal mangrove habitat (Coull et al., 1995), but meiofauna such as harpacticoid copepods and nematodes were either absent or rare in glassfish diets in the present study.

5. Conclusion

Subtropical saltmarsh habitat in Australia has been reduced to a fraction of its former area through agricultural and urban development (Adam, 2002). Where it has been retained, surface water movement is being manipulated to control mosquito populations (Breitfuss et al., 2003, 2004). Models of saltmarsh ecology developed in the northern hemisphere do not necessarily apply to these Australian marshes, which are inundated less often and for shorter periods (Connolly, 2005). It is therefore important to understand the role the marshes have in the functioning of estuaries. Many small fish species and juveniles of larger, economically important fish species visit the marshes of southern Queensland (Thomas and Connolly, 2001). Until now, we have had no understanding of how fish use the marsh. The present study has shown that one of the most abundant fishes in southern Queensland estuaries feeds extensively on the marsh at night, providing a potential trophic link between high intertidal habitat and the rest of the estuary.

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