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Refugees or ravenous predators: detecting predation on new recruits to tropical estuarine nurseries

Ron Baker · Marcus Sheaves

Abstract Many of the most abundant small and juvenile fishes within shallow water estuarine nursery habitats consume other fish to some degree but have rarely been considered as potentially important predators in the functioning of these systems because of the low (<50%) average occurrence of fish in their diets. Predation by abundant minor piscivores on new recruits when they first enter the nursery may make a significant contribution to the predation mortality of this critical life-history stage. To determine the potential importance of minor piscivores as predators on new recruits, temporal patterns in the diets of 15 common species of minor piscivores were examined and related to the abundance of new recruits (≤20 mm FL) in biweekly seine samples over 13 months in shallow (<1.5 m) sandy habitats in the Ross River estuary in north-eastern Queensland, Australia. The high spatial patchiness of new recruits made it difficult to correlate their abundance with their consumption by minor piscivores, and there was no relationship detected between the abundance of new recruits and the occurrence of fish in the diets of minor piscivores.

To gain broader insight into spatio-temporal patterns in the consumption of fish prey by minor piscivores, we utilised a collection of fishes sampled during various studies over 6 years from 17 estuaries in the region to examine the diets of >3500 individuals from 20 spp. of minor piscivores. Patterns in the consumption of fish prey by these minor piscivores, especially the highly abundant sparids, sillaginids and ambassids, revealed that the low average occurrence of fish in their diet greatly underestimated the predation pressure imposed by these on fish prey at particular locations and times. For most sampling occasions and locations few minor piscivores consumed fish prey (consumed by 0% of individuals examined), while occasionally a large proportion of individuals within a taxon did so (50–100% of individuals consumed fish prey). Often at such times/locations multiple species of minor piscivores simultaneously preyed heavily on fish. When minor piscivores consumed fish, they preyed mainly on small new recruits. Because many of these minor piscivores are relatively recent recruits, many of the small and juvenile fishes believed to gain refuge in shallow estuarine nurseries may themselves be important predators on fish subsequently recruiting to these habitats, and so potentially play a significant role in structuring estuarine fish faunas and the functioning of shallow water nurseries.

Keywords Minor piscivore · Nursery ground functioning · Refuge paradigm · Tropical Australia · Gut content analysis

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Introduction

The management and conservation of shallow estuarine habitats is largely driven by the recognition of their role as nurseries for a wide range of ecologically, culturally and economically important species (Boesch and Turner 1984; Beck et al. 2001; Secor and Rooker 2005). These systems are considered valuable nurseries for juvenile fishes and other nekton because they are believed to provide abundant food and refuge from predation. The refuge value of shallow water habitats is widely considered to be due in part to low numbers of predatory fishes (e.g. Blaber and Blaber 1980; McIvor and Odum 1988; Paterson and Whitfield 2000). However, typically only primarily piscivorous fishes have been considered as potentially important predators on other fishes in these systems (e.g. Blaber 1980; Hartman and Brandt 1995). Occasional or 'minor' piscivores, those species that <50% of individuals on average will have consumed fish at any given time (Whitfield and Blaber 1978), have largely been ignored (Sheaves 2001), despite the fact that such fishes are often dominant members of shallow water estuarine assemblages around the globe (e.g. Martin and Blaber 1983; Monteleone and Houde 1992; Edgar and Shaw 1995; Haywood et al. 1998; Maes et al. 2003).

Within tropical and subtropical Indo-Pacific estuaries, abundant minor piscivores include glass-perches (Ambassidae), whiting (Sillaginidae), bream (Sparidae) and small juveniles of species which are primarily piscivorous at larger sizes such as flathead (Platycephalidae) and queenfish (Carangidae) (Robertson and Duke 1990a; Morton 1990; Salini et al. 1990; Haywood et al. 1998; Baker and Sheaves 2005). Glass perch are primarily zooplantivores, while the other abundant minor piscivores mainly prey on benthic invertebrates, but all incorporate fish prey in their diets to some degree (Wilson and Sheaves 2001; Baker and Sheaves 2005). Thus the shallow water refuge paradigm and our understanding of the functioning of estuarine nurseries have overlooked a component of the estuarine fauna which may contribute significant mortality on recruiting fishes (Martin and Blaber 1983) and create bottlenecks in the life history of fishes utilising these habitats (Sheaves 2005).

Early life history stages of fishes suffer massive levels of natural mortality (Sogard 1997). Small changes in early mortality rates can profoundly influence ultimate cohort strength (Levin and Stunz 2005). For example, predation on coral reef fish in the first few hours after settlement can have a significant, long-term influence on cohort survivorship and the structure of reef fish assemblages (Almany 2004). Similarly, predation on new recruits to shallow estuarine nursery habitats has the potential to substantially influence the structure of estuarine fish communities.

Because of the temporally patchy nature of recruitment (Robertson and Duke 1990b), the consumption of new recruits by estuarine predators must also be patchy (Nemerson and Able 2004). Unfortunately, available dietary data on tropical estuarine fishes are usually presented pooled over sampling occasions and locations to provide a simple representation of dietary composition (e.g. Salini et al. 1990; Haywood et al. 1998; Baker and Sheaves 2005). Dietary data presented in this way represent the mean composition of the pooled samples. However, little consideration has been given to the underlying variability in dietary habits when interpreting the importance of various predators on prey populations based on gut content data. By pooling data, information on spatial and temporal variability in diets is lost, including information on details such as prey switching. This is not to say that the available dietary data on predatory estuarine fishes are not useful representations of the importance of various prey types in the overall diets of those predators. However, the predator–prey relationship may be asymmetric such that the importance of prey to the predator does not necessarily reflect the importance of the predator to particular prey (Walters and Martell 2004). Specifically, just because minor piscivores may derive little of their nutrition from fish prey, minor piscivores that prey on new recruits may still be potentially significant sources of mortality for recruiting fishes (Martin and Blaber 1983).

The low average occurrence of fish in the diet of minor piscivores could reflect consumption of alternate prey most of the time, with occasional shifts to heavily consume new recruits when they are periodically abundant during and shortly after recruitment events (e.g. Martin and Blaber 1983; Köster and Möllmann 2000). Detecting such events in estuarine systems is a challenging task given the unpredictable timing and spatially patchy nature of recruitment events at fine temporal scales (Robertson and Duke

1990b), the complex and dynamic nature of habitat use in these systems (Sheaves 2005; Rountree and Able 2007) and the difficulties these present in sampling the fish community (Kneib 1997; Rozas and Minello 1997). Despite the challenge in detecting such things as prey switching, ignoring such events may result in seriously misleading interpretations of the importance of predation in structuring these systems (Edwards et al. 1982; Martin and Blaber 1983; Swain and Sinclair 2000).

The aim of this study was to determine if abundant minor piscivores from tropical estuaries in north-eastern Australia prey heavily on new recruits. If so, abundant minor piscivores may contribute a significant proportion of the predation mortality on vulnerable early life stages of fishes accessing shallow estuarine nursery habitats and thus play an important but largely overlooked role in the functioning of these systems.

Methods

Two approaches were adopted to determine if minor piscivores prey heavily on new recruits. Firstly, the abundance of new recruits and the diets of minor piscivores were monitored intensively over 13 months in the Ross River estuary in north-east Queensland, Australia, to look for direct evidence of a diet shift in response to recruitment events.

Secondly, we examined the gut contents of a large collection of fishes from the Ross River and 16 other estuarine systems in the region sampled during various studies between 1999 and 2004 to gain a broad understanding of the spatio-temporal patterns in the consumption of fish prey by minor piscivores.

Study sites

The estuarine systems sampled extend along 250 km of the tropical north-eastern coast of Queensland, Australia (Fig. 1). The region experiences highly seasonal rainfall with the majority falling during the summer wet season between November and March. The tides are semi-diurnal with a maximum range of ~4 m and most estuaries are fringed by extensive mixed mangrove forests in the upper intertidal. The lower reaches of estuaries in the region are typically dominated by sand substrates while mud substrates dominate upstream. Although several species of sea grasses do occur in estuaries in this region (Coles et al 1987), these generally do not form extensive meadows common in other parts of the world. Thus for the majority of the time small and juvenile nekton occupying shallow waters in the lower reaches of these estuaries are restricted to unvegetated sandy habitats (Johnston and Sheaves 2007).

A number of studies have described the estuarine fish fauna in this region (e.g. Blaber 1980; Robertson and Duke 1990a; Sheaves 2006) and individual

Fig. 1 Estuarine study sites in north-eastern Queensland, Australia
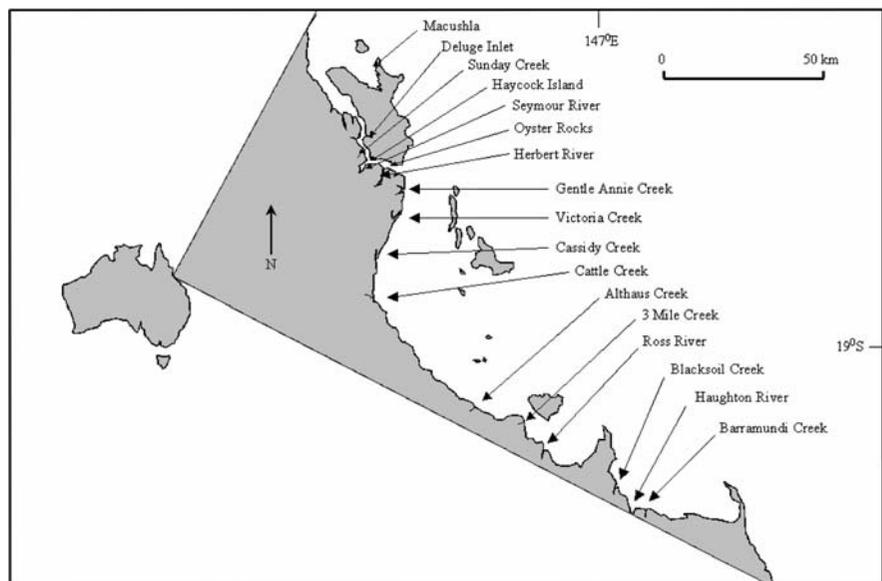
estuaries may contain more than 200 species of fish (Blaber 2000). There is little or no demographic data available for the vast majority of these fishes (Blaber 2000). The only published study on recruitment of juvenile fishes into estuarine nurseries in the tropical Indo-West Pacific (Alligator Creek near Townsville, Australia, 19°21′ S, 146°57′ E) sampled at 7-week intervals and recorded year-round recruitment with a broad peak during the summer wet season between November and April (Robertson and Duke 1990b). Most species showed extended recruitment seasons (≥5 month), with irregular pulses of recruits appearing in the estuary during the 13 month study. New recruits of most species were <20 mm and grew rapidly upon arrival to the estuary (Robertson and Duke 1990b).

Recruitment variability, minor piscivore diets, and prey switching

Recruit abundance and the diets of minor piscivores were monitored during 2001–2002 in the Ross River estuary in north-east Queensland, Australia (Fig. 1). Initially samples were collected every 3–4 days from 27th of February until 29th of March 2001 (9 sampling occasions). Subsequent sampling was conducted biweekly, on new and full moons, from 29th of March 2001 until 29th of March 2002. One full moon sample at the beginning of August 2001 could not be collected. Although biweekly sampling combined with the spatial patchiness of new recruits meant that we would likely fail to detect some recruitment events, it was not logistically feasible to maintain higher levels of sampling effort, and this design provided 33 sampling occasions to examine any correlation between recruit abundance and minor piscivores diets.

Samples were collected in the lower 2 km of the estuary along shallow (≤1.5 m), unvegetated sand banks during daylight hours from the late ebb to slack low tide. On each sampling occasion, five replicate hauls were made using a 6 mm mesh 12 × 2 m seine net hauled for 10 m along the shore. Replicate hauls were located randomly with a minimum of 100 m separation. Recruitment was quantified by summing the abundance of all fish ≤20 mm across all net shots for each sampling occasion. For most of the common taxa from the region including small species such as gobiids, individuals ≤20 mm are recent recruits

(Robertson and Duke 1990b; Sheaves unpub. data). As such, gobiids ≤20 mm were included in counts of new recruits, and these comprised ∼1% of the total number of new recruits sampled. Additional hauls using the same gear were made to supplement samples of predatory fishes for gut content analysis.

The 15 species examined for gut contents (Table 1) were those previously identified as minor piscivores by Wilson and Sheaves (2001) and Baker and Sheaves (2005). Empty guts were not included in analyses because the possibility of regurgitation during capture makes their significance ambiguous (Bowman 1986). The proportion of empty guts for individual taxa ranged from 0 to 25%, and was <10% for 10 of the 15 species examined. Least squares univariate classification and regression tree (CART) analysis was used to examine the relationship between the frequency of occurrence of fish prey in the diets of minor piscivores and recruit abundance on various sampling occasions (De'ath and Fabricius 2000). CART analyses can be used on data that are unbalanced, have missing values, non-linear relationships between variables, and/or high-order interactions. In this analysis, the

Table 1 Sample size and % frequency of occurrence of fish in the diet of minor piscivores sampled from the Ross River, Australia, 2001–2002

Taxon	n	%
Acanthopagrus berda	8	50
Ambassis nalua	1	0
A. telkara	10	0
Lutjanus fulviflamma	4	50
Platycephalus arenarius <45 mm[a]	35	37.1
P. fuscus <50 mm[a]	7	14.3
Pseudorhombus arsius <30 mm[a]	2	100
Sillago analis	24	0
S. burrus	1	0
S. ciliata	4	0
S. sihama	335	0.9
Scomberoides commersonianus <60 mm[a]	10	30
S. lysan <55 mm[a]	22	18.2
cf. *Saurida gracilis*	30	26.7
Suggrundus sp.	8	12.5
Total	501	8.2

n = Number of stomachs containing food, empty stomachs were excluded from analyses

[a] Size classes identified as minor piscivores by Baker and Sheaves (2005)

occurrence of fish in the diet of minor piscivores was the dependant variable, while the predator species identity, the sampling date, and the abundance of new recruits were the explanatory variables. The technique successively splits data into increasingly homogenous groups by minimising the residual sums of squares for each split, analogous to least squares regression (De'ath and Fabricius 2000). Tree branchings indicate variables that explain substantial variability in the occurrence of fish in the diets of minor piscivores. A correlation between the abundance of new recruits and the diet of minor piscivores would be reflected by the explanatory variable of 'recruit abundance' forming one or more splits on the tree, indicating that high abundance of new recruits explains high occurrences of fish in the diet of minor piscivores. The 'best' tree models were chosen by bootstrapped cross validation using both the Min. and Min. + 1 SE rules (Breiman et al. 1984; De'ath and Fabricius 2000).

Spatial patchiness of new recruits

The spatial distribution of new recruits was described by calculating the variance to mean ratio (VMR) of the abundance estimates obtained from the five replicate net hauls on each sampling occasion (Zar 1999). If recruits were randomly distributed on any particular sampling occasion, the variance of the estimate of recruit abundance from the five replicate net shots should approximately equal the mean (VMR = 1). A variance smaller than the mean (VMR < 1) indicates a uniform distribution, while an aggregated distribution would be indicated by large variance relative to the mean recruit abundance estimate (VMR > 1) (Zar 1999).

Spatio-temporal variability in predation by minor piscivores

In addition to the diet data from the Ross River samples, we utilised a large collection of fishes sampled during a number of studies from the Ross River and 16 other estuarine systems in the region spanning 6 years between 1999 and 2004 (Fig. 1), to gain a broader view of spatio-temporal patterns in the consumption of fish prey by minor piscivores. We examined the gut contents of approximately 4000 minor piscivores from 20 taxa. Of these, 12.7% had empty guts and were excluded for further analysis,

leaving a sample size of >3500 individuals that contained food. The percentage of empty guts for individual taxa was generally low and ranged from 0 to 26%.

The minor piscivore assemblage was numerically dominated by various *Sillago* spp. (Sillaginidae), *Ambassis* spp. (Ambassidae), *Acanthopargus* spp. (Sparidae) as well as small juveniles of species known as piscivores at larger sizes including *Platycephalus* spp. (Platycephalidae) and *Scomberoides* spp. (Carangidae). For details of field sampling see Wilson and Sheaves (2001); Baker and Sheaves (2005); Sheaves (2006), and Johnston and Sheaves (2007). In brief, minor piscivores were collected for gut content analysis from shallow (≤1.5 m) sandy habitats in the lower reaches (≤5 km) of each estuary. Collections were made from the 17 estuaries on a total of 198 occasions, covering 35 of the 55 month of the sampling period, including samples representing every month of the year.

Minor piscivores were species with <50% average frequency of occurrence of fish in their diets (Whitfield and Blaber 1978). Spatio-temporal patterns in the consumption of fish by common minor piscivores identified by Baker and Sheaves (2005) (including the smaller size classes of major piscivores which did not prey heavily on fish at small sizes) were examined. The frequency of occurrence of fish in the diet of minor piscivores was calculated for individual sampling occasions. Spatio-temporal variability in the consumption of fish prey was examined by constructing histograms showing the frequency of samples of minor piscivores with different levels of fish in the diet. The mean occurrence of fish across the pooled samples is indicated on each histogram to allow an assessment of how well the pooled or average diet represents spatio-temporal patterns in the consumption of fish prey. To avoid the over-interpretation of small sample sizes while concurrently retaining potentially informative data, only samples that contained ≥4 individuals were included when constructing the histograms. As such the samples depicted in the histograms represent a subset of the entire data set. Higher than average occurrences of fish in the diet of minor piscivore taxa on particular sampling occasions were cross-referenced among all the minor piscivore taxa sampled at the same location/time to look for evidence of multiple species switching to fish prey.

Prey size and identity

Where possible fish prey in the guts of minor piscivores were identified and measured (fork length [FL] in millimetres). In the case of highly digested prey, fish were identified using a catalogue of sagittal otoliths, and prey lengths were estimated from otolith-weight/fish-length relationships calculated from prey fish collected from the same estuaries (Baker 2006b). Otoliths showing signs of digestion were not used to estimate prey length (see Baker and Sheaves 2005).

Results

Recruitment variability, minor piscivore diets, and prey switching

A total of 69,395 individuals from 127 taxa of nektonic organisms were sampled from the Ross River, including 51,561 individuals from 120 taxa of fish, 17,800 crustaceans from 6 taxa (83% were *Acetes*) and 34 squid (cephalopoda). Of the fish, 14,804 were ≤20 mm FL and considered as new recruits. Reflecting the overall catch composition, the recruit assemblage was dominated by the Leiognathidae, Sillaginidae, and Gerreidae. Four taxa, *Leiognathus splendens*, *Sillago* spp. juveniles, *Leiognathus* spp. juveniles, and *Secutor ruconius*

made up more than 90% of the total number of new recruits. Recruitment was highly variable over time, however at least some new recruits (≤20 mm FL) were sampled on every sampling occasion over the 13 month study (minimum $n = 2$, 30/12/01) (Fig. 2). The largest sample (10,599 recruits on 13th of March 2001) primarily comprised *Leiognathus* spp. The sample of 629 recruits on March 29th 2001 was a mixture of *Sillago* spp., *Leiognathus* spp. and *Gerres* spp., while the 868 new recruits sampled on May 23rd were mainly *Sillago* spp.

A total of 501 individuals from 15 taxa of common minor piscivores sampled from the Ross River were examined for gut contents and contained food (Table 1). Each of these predators normally consume benthic invertebrates or planktonic crustaceans (Wilson and Sheaves 2001; Baker and Sheaves 2005). Forty-one minor piscivores (8.2% of total sample) from 10 taxa were found to have consumed fish prey. CART analysis detected no relationships between the measured recruit abundance and the occurrence of fish in minor piscivore diets, regardless of the combination of explanatory variables (recruit abundance, predator identity, sampling date) or method of selecting the 'best' model. This indicates that while various species consumed fish prey on various occasions (Table 1), there was no detectable relationship between the consumption of fish prey and the measured abundance of new recruits (Fig. 2).

Fig. 2 Abundance of new recruits (≤20 mm FL) and % frequency of occurrence of fish prey in the diets of minor piscivores in samples from the mouth of the Ross River, 27th February 2001–29th March 2002
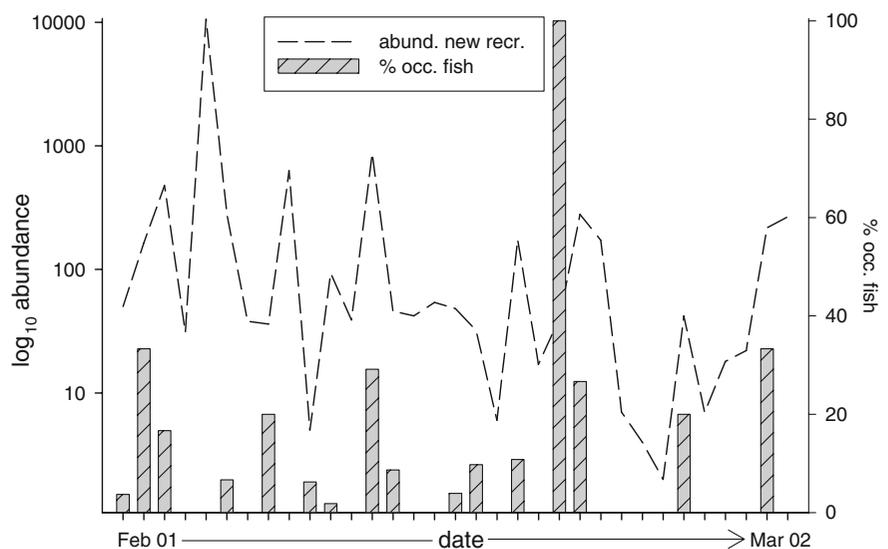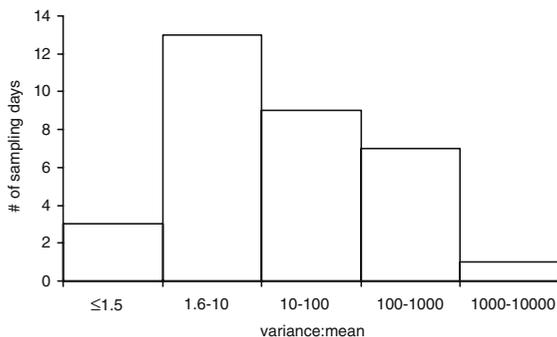
Spatial patchiness of new recruits

Spatially, new recruits were highly aggregated. On most sampling occasions the variance in abundance estimates from the five replicate net samples were orders of magnitude greater than the mean (Fig. 3 and Table 2). On the only three occasions when the variance to mean ratio indicated the possibility of either a random or uniform distribution of recruits (VMR ≤ 1.5), very few recruits were recorded (Table 2).

Spatio-temporal variability in fish predation by minor piscivores

Among the minor piscivores sampled from the 17 estuaries throughout the region, the low average occurrence of fish in the diet was invariably a poor representation of spatial and temporal patterns in their consumption of fish prey (Fig. 4). On most sampling occasions, none or very few individuals

examined for gut contents had consumed fish prey, while occasionally a large proportion of individuals had done so. Within particular estuaries on certain sampling occasions, multiple minor piscivore species had an above average occurrence of fish prey in the diet (Table 3). For example, four of the six species of minor piscivores sampled from Victoria Creek in November 1999 had a higher than average occurrence of fish in the diet (Table 3).

When minor piscivores consumed fish prey, they fed mainly on small new recruits (Fig. 5). Identifiable fish prey were mostly *Leiognathus* spp., *Sillago* spp. and *Gerres* spp. ≤20 mm. Few individuals had consumed fish prey larger than 20 mm (Fig. 5a, f, g, h). Fish prey in the guts of minor piscivores not shown in Fig. 5 were mostly small new recruits. While some unidentified fish prey may have been individuals of small species such as gobiids, most common local gobiids <20 mm are also relatively new recruits to the shallow water habitats sampled (Baker and Sheaves pers. obs.).

Discussion

Correlating abundance and diet in an inherently patchy system

There was no relationship between the abundance of new recruits and the occurrence of fish in the diets of minor piscivores in the Ross River during 2001–2002. This indicates that either (1) the minor piscivores did not shift diets in response to recruitment events, or (2) they did but this was not detected. Given the highly aggregated distribution of recruits within the shallow water habitats sampled (Fig. 3 and

Fig. 3 Distribution of variance to mean ratio in the abundance estimates of new recruits from five replicate nets on each sampling occasion, Ross River, 2001–2002

Table 2 Spatial variability in the abundance of new recruits (≤20 mm) in replicate samples from shallow sandy habitats in the mouth of the Ross River

VMR is the variance to mean ratio. Shown are the three sampling dates with the highest recorded recruit abundance, and three dates with the lowest VMR

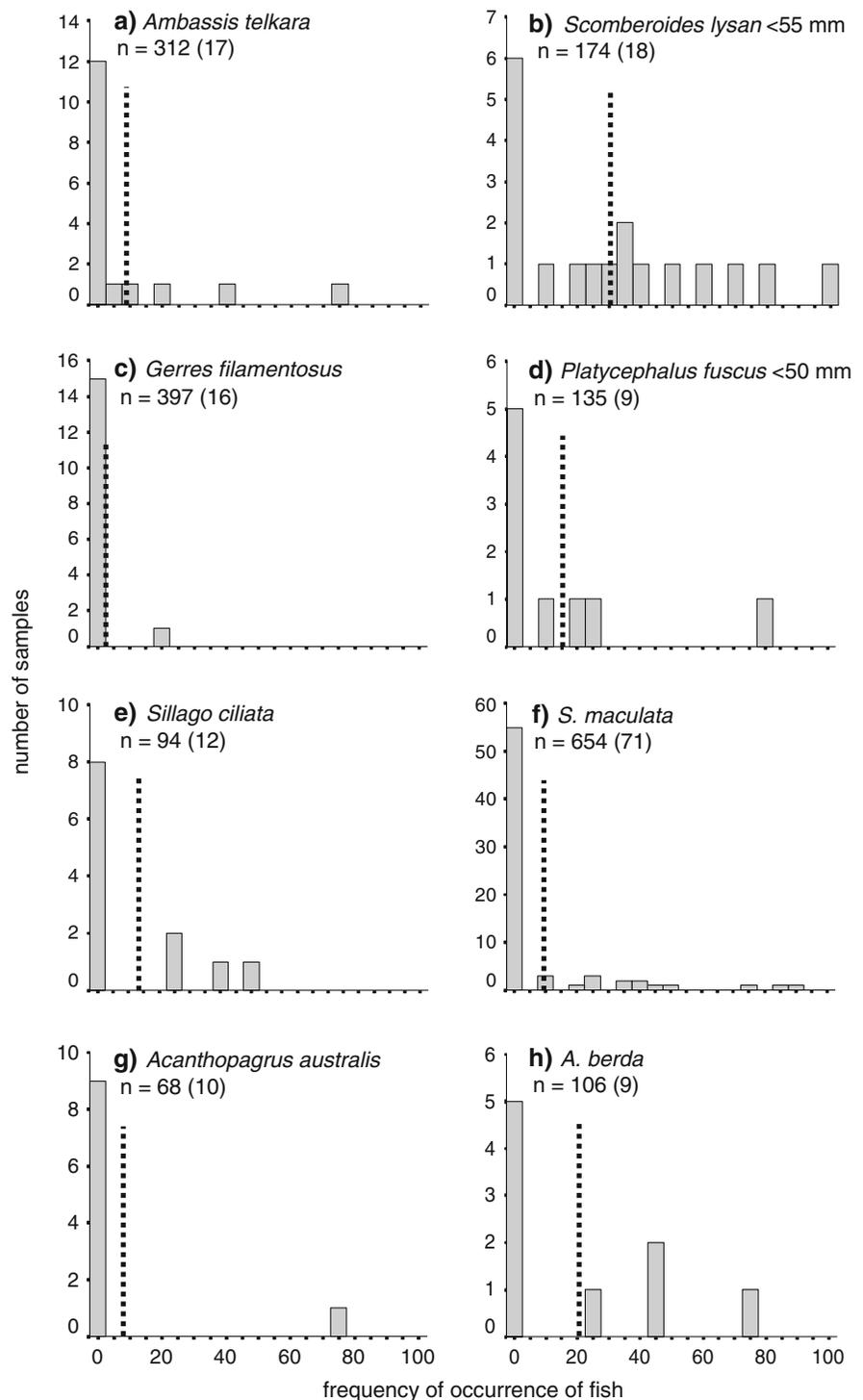| Sample	14/03/01	25/03/01	29/03/01	23/05/01	03/09/01	30/12/01
1	134	2	317	66	2	0
2	10,285	8	0	750	2	1
3	139	7	0	52	2	0
4	37	11	35	0	0	0
5	4	8	277	0	0	1
N	10,599	36	629	868	6	2
Mean	2119.8	7.2	125.8	173.6	1.2	0.4
St. dev.	4564.9	3.3	157.6	323.6	1.1	0.5
VMR	9830	1.5	197	603	1.0	0.8

Table 2), it seems unlikely that the measured recruit abundance would have been representative of the abundance of fish prey encountered by the minor piscivores (Walters and Martell 2004). Although recruitment was only quantified in one system during this study, high spatial patchiness of estuarine fishes in shallow water habitats is a widespread phenomenon (Rozas and Minello 1997; Minello and Rozas

Table 3 Spatio-temporal overlap in the consumption of fish prey by minor piscivores in estuaries of north-eastern Queensland, Australia

Estuary	Date	Acanthopagrus australis	A. berda	Ambassis telkara	Gerres filamentosus	Platycephalus fuscus <50 mm	Scomberoides lysan <55 mm	Sillago analis	S. ciliata	S. maculata	S. sihama
Deluge	Nov 99	0/4	0/3	0/6	0/38	–	0/20	–	–	1/4	0/18
Herbert	Jul 01	1/2	0/4	–	–	0/3	–	0/1	–	–	–
Gentle Annie	Nov 99	0/1	–	0/61	2/11	–	9/22	–	0/7	2/12	0/80
Victoria	Nov 99	1/3	–	3/8	0/16	–	5/11	–	–	6/21	0/5
Victoria	Jul 00	–	–	–	–	0/4	–	1/9	1/2	0/22	–
Victoria	Sep 00	–	4/9	2/5	–	4/5	1/2	–	0/1	13/39	1/2
Victoria	Nov 01	–	0/1	–	–	–	2/6	–	1/2	1/2	0/1
Cassidy	Nov 99	6/8	–	0/28	0/31	–	2/4	–	–	–	0/4
Cassidy	Nov 01	–	3/4	–	–	–	5/5	1/3	2/8	4/16	2/2
3 Mile	Nov 01	–	1/4	0/2	–	–	1/1	1/2	–	0/1	–
Ross	May 00	–	–	11/15	–	6/54	–	1/17	0/5	–	2/54
Ross	Nov 01	–	3/7	0/2	–	–	2/9	0/2	0/1	0/1	0/1
Blacksoil	Nov 99	0/1	0/1	3/14	0/32	–	25/35	0/27	4/10	6/20	1/6
Blacksoil	Jul 00	0/2	0/1	–	–	–	–	0/4	0/4	0/4	1/12
Blacksoil	Jul 01	2/2	–	–	–	–	–	0/1	1/8	0/8	0/7
Blacksoil	Nov 01	–	–	0/1	–	–	14/17	0/1	3/5	10/17	1/1
Haughton	Nov 01	–	1/1	0/7	–	2/2	0/7	–	–	–	–
Barramundi	Nov 99	0/4	0/3	0/22	0/60	1/3	0/1	0/1	1/3	–	1/15

Data represent the fraction of individuals in which fish prey occurred. For example, in Deluge Inlet, November 1999, none of the four *A. australis* examined for gut contents had consumed fish prey. Data are presented only for spp. which occurred on at least 10 sampling occasions, and dates with at least 4 spp. of minor piscivores examined for gut contents

Fig. 5 Size and identity of fish prey in the diets of minor piscivores from estuaries in north-eastern Queensland, Australia. Predator sample size, n = the number of individuals, followed in parenthesis by the number of sampling occasions from which they were collected
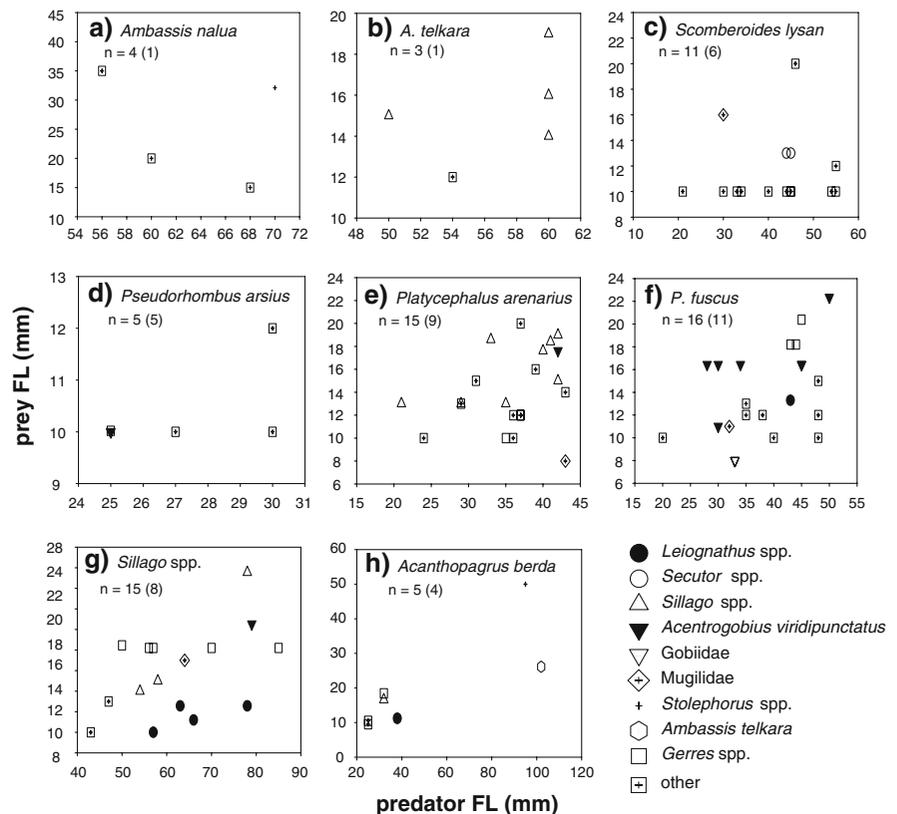
2002; Nemerson and Able 2004; Sheaves 2005; Rountree and Able 2007).

The patchiness in both predators and prey means that may not be possible to directly detect prey switching by correlating recruit abundance with predator diets because a correlation implicitly assumes that the abundance of recruits sampled represents the abundance of fish prey available to the predators in the foraging period prior to their capture. Predator diets and the measured recruit abundance will be decoupled when recruits are spatially patchy at scales covered by foraging predators (Marchand et al. 1999). In this case, although patches of recruits are present in an area, the sampled minor piscivores may not have encountered the recruits. On other occasions, predators which have encountered and consumed recruits will be captured, while the recruits themselves will be missed. Even when both predators that have consumed fish prey, and the fish prey themselves are sampled, there is no way of determining how accurately the samples represent the availability of fish prey to the predators sampled. Although it may be possible to quantify the

spatial patchiness of the recruits, it is very challenging to quantify the spatial distribution of minor piscivores during the foraging period represented by their gut contents. It takes around 6 h for fish prey to digest or pass through the stomach of small predatory fishes from estuaries in north-eastern Queensland (Baker 2006a), and determining the area covered by a small fish inhabiting intertidal estuarine habitats over a six hour period is highly problematic (Rozas and Minello 1997; Sheaves 2005; Rountree and Able 2007). Furthermore, interpretations of the spatial significance of the gut contents will be confounded by the behaviours of both predator and prey during encounters between the two (Manderson et al. 2000; Juanes et al. 2001).

It could be argued that the failure to detect a relationship between recruit abundance and minor piscivore diets in Ross River simply reflects a flawed sampling design. Indeed, greater replication or more appropriate replicate size could potentially reduce the error in the recruit abundance estimates and provide a better representation of their spatial distribution (McBride et al. 1995; Rozas and Minello 1997).

However, no sampling design can overcome the inherent patchiness of the system. Regardless of the sampling design, if the prey resource encountered by the predator is patchy (Rozas and Minello 1997; Nemerson and Able 2004; this study), it will be very difficult to correlate prey abundance with predator diet (e.g. Marchand et al. 1999).

Despite the failure to directly detect prey switching in response to recruitment events, the indirect evidence provided by detailed examination of spatial and temporal patterns in the consumption of fish prey is indicative of minor piscivores switching from a non-fish diet to prey heavily on new recruits during recruitment events.

Indirect evidence of prey switching

The low average occurrence of fish in the diets of minor piscivores (Baker and Sheaves 2005; Table 1 this study) was a poor representation of the spatial and temporal patterns in predation pressure by these on fish prey (Fig. 4). Most of the time, none or few of the minor piscivores examined had consumed fish prey, while occasionally a large proportion of individuals had done so (Fig. 4 and Table 3). When they consumed fish, they preyed mainly on new recruits (Fig. 5), which are only available in high abundance occasionally because of the temporally patchy nature of recruitment (Robertson and Duke 1990b; Fig. 2 this study). While the sample sizes of individual species of minor piscivores examined for gut contents on any particular sampling occasion may be small and uneven (thereby precluding formal statistical analyses), multiple species of minor piscivore all preying on recruits simultaneously provides a strong indication of a shift in minor piscivore diets to prey on recruits in response to recruitment events (Table 3). Thus the low average occurrence of fish regularly reported in the diets of minor piscivores may represent the consumption of alternate prey for most of the time with the occasional high consumption of new recruits during recruitment events when this profitable food source is in high abundance (Martin and Blaber 1983).

The spatio-temporal variability in the consumption of fish prey highlights the difficulty in interpreting the pooled diet data previously used to infer the importance of various predators on prey fish populations (Blaber 1980; Salini et al 1990). Not only is the mean diet potentially a poor representation of the impacts

on patchy prey resources (Fig. 4), the values recorded will be dependant on the spatial and temporal distribution of the samples collected for dietary analysis. The dietary composition of a sample of individuals collected from one place at one time represents something different to that of a similar sized sample collected from many locations at many times, yet pooled dietary data allows no distinction between these scenarios even though the implications of the dietary composition are quite different. Finally, if the underlying shape of the distribution of the consumption of fish prey is unknown, then interpreting the level of consumption of fish prey based only on the mean will be potentially invalid and misleading. For example, if minor piscivores consumed fish prey at some constant low level (i.e. the distributions shown in Fig. 4 were approximately normal), then the mean occurrence of fish in the diet would be a reasonable representation of their level of consumption of new recruits to estuarine nurseries. Clearly, however, this is not the case.

Implications for levels of predation and nursery functioning

The minor piscivores examined in this study, such as ambassids, sillaginids and sparids, are common throughout tropical and sub-tropical Indo-Pacific (e.g. Morton 1990; Salini et al. 1990; Haywood et al. 1998). Globally, minor piscivores are often among the most abundant fish taxa sampled from shallow water estuarine habitats, and many are themselves small juvenile fishes utilising shallow water nurseries (Monteleone and Houde 1992; Edgar and Shaw 1995; Haywood et al. 1998; Maes et al. 2003). Consequently, alternate food sources maintain a large abundance and biomass of predatory fishes in shallow nursery habitats (Wilson and Sheaves 2001), which potentially prey heavily on new recruits when they enter the system.

The level of refuge provided by shallow nursery habitats in tropical estuaries of NE Australia, and elsewhere in the world, may have been overestimated because of the assumption that the low average levels of predation by minor piscivores reflect the levels of impact of these predators on prey fish populations (e.g. Whitfield and Blaber 1978; Blaber 1980; Salini et al. 1990). An intense pulse of predation on early life stages could significantly influence cohort

survivorship (Yanez-Arancibia et al. 1994; Levin and Stunz 2005) and the structure of estuarine fish assemblages just as it does in other systems such as coral reefs (e.g. Carr and Hixon 1995; Webster 2002; Almany 2004) and pelagic waters (e.g. Ellis and Nash 1997; Köster and Möllmann 2000; Swain and Sinclair 2000).

In estuarine systems, pulse events, such as predation on new recruits, are difficult to predict and detect (Robertson and Duke 1990b; Sheaves 2005; Rountree and Able 2007). Shallow water nursery assemblages mainly utilise intertidal habitats and are thus constantly moving in response to tidal fluctuations (Rozas and Minello 1997; Nemerson and Able 2004; Sheaves 2005; Rountree and Able 2007). Because of this, abundance estimates are highly variable (Rozas and Minello 1997; Rountree and Able 2007; Table 2 this study) and monitoring changes in abundance through time to estimate mortality, as is done with site-attached species on coral reefs (e.g. Almany 2004), is not possible (Rountree and Able 2007). Examining gut contents of predatory fishes is one way to detect and measure predation mortality (Buckel et al. 1999; Rountree and Able 2007), however this approach is limited by the length of time it takes to digest prey (Haywood 1995). A predation event on new recruits entering an estuary on one incoming tide may inflict massive mortality (Martin and Blaber 1983) but only be detectable for a few hours following the event (Haywood 1995; Baker 2006a). The difficulty in detecting unpredictable, sporadic events makes them easy to overlook, however assuming such events to be insignificant may lead to serious misinterpretations of the processes structuring estuarine fish assemblages (Edwards et al. 1982; Köster and Möllmann 2000; Sheaves 2005). Despite the lack of direct evidence from the Ross River study of prey switching by minor piscivores in response to recruitment events, we believe the indirect evidence strongly suggests that these may be a significant component of the piscivore assemblage that preys on vulnerable new recruits. We hope these findings will stimulate further consideration and investigation of the role these largely overlooked predators play in the functioning of shallow estuarine nursery habitats.

References

Almany GR (2004) Priority effects in coral reef fish communities of the Great Barrier Reef. Ecology 85:2872–2880. doi:10.1890/03-3166

Baker R (2006a) Piscivory and the functioning of shallow tropical estuarine nursery grounds. PhD Dissertation, James Cook University, Townsville

Baker R (2006b) Otolith catalogue of common coastal and estuarine fishes of north-eastern Queensland, Australia. James Cook University, Townsville. Available online at: http://www.jcu.edu.au/school/mbiolaq/ind_labs/estecol/papers.htm

Baker R, Sheaves M (2005) Redefining the piscivore assemblage of shallow estuarine nursery habitats. MEPS 291:197–213. doi:10.3354/meps291197

Beck M, Heck K, Able K, Childers D, Eggleston D, Gillanders B, Halpern B, Hays C, Hoshino K, Minello T, Orth R, Sheridan P, Weinstein M (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. Bioscience 51:633–641

Blaber SJM (1980) Fish of the Trinity Inlet system of north Queensland with notes on the ecology of fish faunas of tropical Indo-Pacific estuaries. Aust J Mar Freshwater Res 31:137–146. doi:10.1071/MF9800137

Blaber SJM (2000) Tropical estuarine fishes: ecology, exploitation and conservation. Blackwell Science, Oxford

Blaber SJM, Blaber TG (1980) Factors affecting the distribution of juvenile estuarine and inshore fish. J Fish Biol 17:143–162. doi:10.1111/j.1095-8649.1980.tb02749.x

Boesch D, Turner RE (1984) Dependence of fishery species on salt marshes: the role of food and refuge. Estuaries 7:460–468. doi:10.2307/1351627

Bowman RE (1986) Effect of regurgitation on stomach content data of marine fishes. Environ Biol Fishes 16:171–181. doi:10.1007/BF00005169

Breiman L, Friedman JH, Olshen RA et al (1984) Classification and regression trees. Wadsworth International Group, California

Buckel JA, Conover DO, Steinberg ND et al (1999) Impact of age-0 bluefish (*Pomatomus saltatrix*) predation on age-0 fishes in the Hudson River estuary: evidence for density-dependant loss of juvenile striped bass (*Morone saxatilis*). Can J Fish Aquat Sci 56:275–287. doi:10.1139/cjfas-56-2-275

Carr MH, Hixon MA (1995) Predation effects on early post-settlement survivorship of coral-reef fishes. Mar Ecol Prog Ser 124:31–42. doi:10.3354/meps124031

Coles RG, Lee Long WJ, Squire BA, Squire LC, Bibby JM (1987) Distribution of seagrasses and associated juvenile commercial penaeid prawns in north-eastern Queensland waters. Aust J Mar Freshwater Res 38:103–119. doi:10.1071/MF9870103

De'ath G, Fabricius KE (2000) Classification and regression trees: a powerful yet simple technique for ecological analysis. Ecology 81:3178–3192

Edgar GJ, Shaw C (1995) The production and trophic ecology of shallow-water fish assemblages in southern Australia 1. Species richness, size-structure and production of fishes in Western Port, Victoria. J Exp Mar Biol Ecol 194:53–81. doi:10.1016/0022-0981(95)00083-6

Edwards DC, Conover DO, Sutton F (1982) Mobile predators and the structure of marine intertidal communities. Ecology 63:1175–1180. doi:10.2307/1937256

Ellis T, Nash RDM (1997) Predation by sprat and herring on pelagic fish eggs in a plaice spawning area in the Irish Sea. J Fish Biol 50:1195–1202. doi:10.1111/j.1095-8649.1997.tb01647.x

Hartman KJ, Brandt SB (1995) Predatory demand and impact of striped bass, bluefish, and weakfish in the Chesapeake Bay: Applications of bioenergetics models. Can J Fish Aquat Sci 52:1667–1687. doi:10.1139/f95-759

Haywood MDE (1995) Rates at which post-larval prawns are digested by a small predatory fish and the implications for dietary studies. J Fish Biol 47:337–340. doi:10.1111/j.1095-8649.1995.tb01901.x

Haywood MDE, Heales DS, Kenyon RA et al (1998) Predation of juvenile tiger prawns in a tropical Australian estuary. Mar Ecol Prog Ser 162:201–214. doi:10.3354/meps162201

Johnston R, Sheaves M (2007) Small fish and crustaceans demonstrate a preference for particular small-scale habitats when mangrove forests are not accessible. J Exp Mar Biol Ecol 353:164–179

Juanes F, Buckel JA, Scharf FS (2001) Predatory behaviour and selectivity of a primary piscivore: comparison of fish and non-fish prey. Mar Ecol Prog Ser 217:157–165. doi:10.3354/meps217157

Kneib RT (1997) The role of tidal marshes in the ecology of estuarine nekton. Oceanogr Mar Biol Ann Rev 35:163–220

Köster FW, Möllmann C (2000) Trophodynamic control by clupeid predators on recruitment success in Baltic cod? ICES J Mar Sci 57:310–323. doi:10.1006/jmsc.1999.0528

Levin PS, Stunz GW (2005) Habitat triage for exploited fishes: can we identify essential "essential fish habitat"? Estuar Coast Shelf Sci 64:70–78. doi:10.1016/j.ecss.2005.02.007

Maes J, Brabandere L, Ollevier F et al (2003) The diet and consumption of dominant fish species in the upper Scheldt estuary, Belgium. J Mar Biol Assoc UK 83:603–612. doi:10.1017/S0025315403007537h

Manderson JP, Phelan BA, Stoner AW et al (2000) Predator-prey relations between age-1 + summer flounder (*Paralichthys dentatus*, Linnaeus) and age-0 winter flounder (*Pseudopleuronectes americanus*, Walbaum): predator diets, prey selection, and effects of sediments and macrophytes. J Exp Mar Biol Ecol 251:17–39. doi:10.1016/S0022-0981(00)00191-X

Marchand C, Simard Y, Gratton Y (1999) Concentration of capelin (*Mallotus villosus*) in tidal upwelling fronts at the head of the Laurentian Channel in the St. Lawrence

Estuary. Can J Fish Aquat Sci 56:1832–1848. doi:10.1139/cjfas-56-10-1832

Martin TJ, Blaber SJM (1983) The feeding ecology of Ambassidae (Osteichthyes: Perciformes) in Natal estuaries. S Afr J Zool 18:353–362

McBride RS, Scherer MD, Powell JC (1995) Correlated variations in abundance, size, growth and loss rates of age-0 bluefish in a southern New England estuary. Trans Am Fish Soc 124:898–910. doi:10.1577/1548-8659(1995)124<0898:CVIASG>2.3.CO;2

McIvor CC, Odum WE (1988) Food, predation risk, and microhabitat selection in a marsh fish assemblage. Ecology 69:1341–1351. doi:10.2307/1941632

Minello TJ, Rozas LP (2002) Nekton in Gulf coast wetlands: fine scale distributions, landscape patterns, and restoration implications. Ecol Appl 12:441–455. doi:10.1890/1051-0761(2002)012[0441:NIGCWF]2.0.CO;2

Monteleone DM, Houde ED (1992) Vulnerability of striped bass *Morone saxatilis* (Waldbaum) eggs and larvae to predation by juvenile white perch *Morone americana* (Gmelin). J Exp Mar Biol Ecol 158:93–104. doi:10.1016/0022-0981(92)90310-7

Morton RM (1990) Community structure, density and standing crop of fishes in a subtropical Australian mangrove area. Mar Biol (Berl) 105:385–394. doi:10.1007/BF01316309

Nemerson DM, Able KW (2004) Spatial patterns in diet and distribution of juveniles of four fish species in Delaware Bay marsh creeks: factors influencing fish abundance. Mar Ecol Prog Ser 276:249–262. doi:10.3354/meps276249

Paterson AW, Whitfield AK (2000) Do shallow-water habitats function as refugia for juvenile fishes? Estuar Coast Shelf Sci 51:359–364. doi:10.1006/ecss.2000.0640

Robertson AI, Duke NC (1990a) Mangrove fish-communities in tropical Queensland, Australia: spatial and temporal patterns in densities, biomass and community structure. Mar Biol (Berl) 104:369–379. doi:10.1007/BF01314339

Robertson AI, Duke NC (1990b) Recruitment, growth and residence time of fishes in a tropical Australian mangrove system. Estuar Coast Shelf Sci 31:723–743. doi:10.1016/0272-7714(90)90022-J

Rountree RA, Able KW (2007) Spatial and temporal habitat use patterns for salt marsh nekton: implications for ecological functions. Aquat Ecol 41:25–45. doi:10.1007/s10452-006-9052-4

Rozas LP, Minello TJ (1997) Estimating densities of small fishes and decapod crustaceans in shallow estuarine habitats: a review of sampling design with focus on gear selection. Estuaries 20:199–213. doi:10.2307/1352731

Salini JP, Blaber SJM, Brewer DT (1990) Diets of piscivorous fishes in a tropical Australian estuary, with special reference to predation on penaeid prawns. Mar Biol (Berl) 105:363–374. doi:10.1007/BF01316307

Secor H, Rooker JR (2005) Connectivity in the life histories of fishes that use estuaries. Estuar Coast Shelf Sci 64:1–3. doi:10.1016/j.ecss.2005.02.001

Sheaves M (2001) Are there really few piscivorous fishes in shallow estuarine habitats? Mar Ecol Prog Ser 222:279–290. doi:10.3354/meps222279

Sheaves M (2005) Nature and consequences of biological connectivity in mangrove systems. Mar Ecol Prog Ser 302:293–305. doi:10.3354/meps302293

Sheaves M (2006) Scale dependent variation in composition of fish fauna among sandy tropical estuarine embayments. Mar Ecol Prog Ser 310:173–184. doi:10.3354/meps310173

Sogard SM (1997) Size-selective mortality in the juvenile stage of teleost fishes: a review. Bull Mar Sci 60:1129–1157

Swain DP, Sinclair AF (2000) Pelagic fishes and the cod recruitment dilemma in the Northwest Atlantic. Can J Fish Aquat Sci 57:1321–1325. doi:10.1139/cjfas-57-7-1321

Walters CJ, Martell SJD (2004) Fisheries ecology and management. Princeton Univesity Press, Princeton

Webster MS (2002) Role of predators in the early post-settlement demography of coral reef fishes. Oecologia 131:52–60

Whitfield AK, Blaber SJM (1978) Food and feeding ecology of piscivorous fishes at Lake St Lucia, Zululand. J Fish Biol 13:675–691. doi:10.1111/j.1095-8649.1978.tb03481.x

Wilson JP, Sheaves M (2001) Short-term temporal variations in taxonomic composition and trophic structure of a tropical estuarine fish assemblage. Mar Biol (Berl) 139:787–796. doi:10.1007/s002270100624

Yanez-Arancibia A, Dominguez A, Pauly D (1994) Coastal lagoons as fish habitats. In: Kjerfve B (ed) Coastal lagoon processes. Elsevier, Amsterdam, pp 363–376

Zar JH (1999) Biostatistical analysis, 4th edn. Prentice Hall International, Sydney