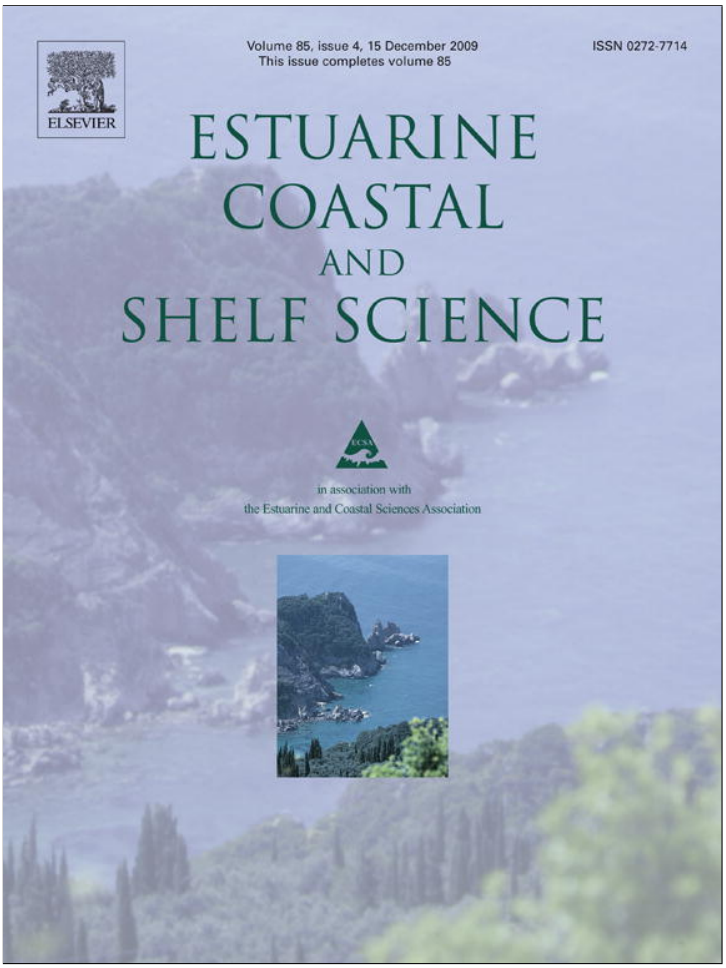
Provided for non-commercial research and education use.
Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

http://www.elsevier.com/copyright

Author's personal copy

Estuarine, Coastal and Shelf Science 85 (2009) 618–626

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Overlooked small and juvenile piscivores dominate shallow-water estuarine "refuges" in tropical Australia

Ron Baker [a,b,*], Marcus Sheaves [a,b]

[a] Coastal and Estuarine Ecosystem Ecology Group, School of Marine and Tropical Biology, James Cook University, Townsville Q 4811 Australia
[b] Coastal CRC, Indooroopilly Sciences Centre, 80 Meiers Road, Indooroopilly Q 4068 Australia

ARTICLE INFO

Article history:
Received 27 February 2009
Accepted 6 October 2009
Available online 13 October 2009

Keywords:
nursery grounds
tropical estuary
recruitment
stomach content analysis
predation

Regional terms:
Australia
tropical north-eastern Queensland

ABSTRACT

A model was developed to estimate the relative impacts of different functional groups of piscivores on the shallow-water estuarine nursery assemblage of tropical north-eastern Australia. Data on variability in the occurrence, number and type of fish in the diet of different piscivores was combined with estimates of the abundance of each group. The model predicts that previously overlooked small and occasional or 'minor' piscivores, such as sillaginids, ambassids, sparids and small juvenile carangids, inflict mortality on new recruits to shallow-water nursery habitats that is orders of magnitude greater than that imparted by more conspicuous larger piscivores. Because of their high abundance, a shift in the diet of minor piscivores to prey on new recruits results in a massive increase in the consumption of fish prey by the piscivore assemblage as a whole. Even if the evidence that minor piscivores switch to target new recruits was rejected, the model shows that the highly abundant minor piscivores must still exert a significant proportion of predation mortality experienced by recruiting fishes. As a broad functional group, minor piscivores occur in most aquatic systems around the globe and are likely to play an important but largely overlooked role as predators that shape communities through predation on critical early life stages of other fishes.

© 2009 Elsevier Ltd. All rights reserved.

1. Introduction

Around the globe, shallow-water estuarine habitats are believed to provide refuge from predation for juvenile nekton utilising these habitats as nurseries (Blaber, 1980; Boesch and Turner, 1984; Paterson and Whitfield, 2000; Deegan et al., 2000). Shallow tropical estuarine nurseries of the Indo-west Pacific contain a diverse assemblage of piscivorous fishes (Blaber, 1986; Salini et al., 1990, 1998; Haywood et al., 1998), including many small (<100 mm) and juvenile fishes that until recently had received little consideration as predators (Sheaves, 2001; Baker and Sheaves, 2005, 2009). The larger, more conspicuous predatory taxa such as belonids, carangids, platycephalids and sphyraenids, are widely recognised as important piscivores within these systems (Blaber, 1986; Salini et al., 1990, 1998; Haywood et al., 1998; Baker and Sheaves, 2006). Fish dominate the diets of these predators (Salini et al., 1990; Baker and Sheaves, 2005) and large individuals of some species are capable of consuming fish prey in great numbers (Baker and Sheaves, 2005). However, many of the highly abundant small and juvenile fishes occupying shallow-water habitats within these systems, such as ambassids, sillaginids and sparids, also consume fish prey to some degree (Salini et al., 1990; Haywood et al., 1998; Baker and Sheaves, 2005). Thus the very fishes believed to gain refuge in shallow-water habitats may themselves be a significant but largely overlooked component of the estuarine piscivore assemblage that preys on new recruits (Baker and Sheaves, 2009).

Because large piscivores primarily consume fish, their abundance and biomass is limited by, and must be considerably less than, that of the assemblage of fishes lower in the food chain. The lower trophic levels, which incorporate small amounts of fish prey in their diets, are maintained at high abundance by alternate food sources and may periodically switch to prey heavily on new recruits during recruitment events when this profitable food source is highly abundant (Baker and Sheaves, 2009). Heavy predation on early life stages of fishes can have a significant influence on the structure of fish communities (Webster, 2002). Population modelling shows that mortality rates of newly recruited fishes can be far more significant than those of older life stages in regulating cohort strength and thus recruitment to the reproductive parent stock (e.g. Levin and Stunz, 2005). Consequently the highly abundant minor piscivores have the potential to contribute significantly to the

* Corresponding author. Present address: NOAA Fisheries Service, SEFSC Galveston Laboratory, 4700 Avenue U, Galveston, TX 77551 USA.
E-mail address: ronnie.baker@noaa.gov (R. Baker).

0272-7714/$ – see front matter © 2009 Elsevier Ltd. All rights reserved.
doi:10.1016/j.ecss.2009.10.006

Author's personal copy

predation pressure experienced by new recruits and play an important role in regulating populations and in the functioning of estuarine nurseries (Baker and Sheaves, 2009).

The aim of this study is to determine the relative importance of different functional groups within the diverse piscivore assemblage that preys on juvenile fishes, and particularly new recruits, using shallow estuarine nursery habitats in tropical north-eastern Australia. To achieve this, a model is developed to estimate the relative magnitude of potential consumption of fish prey by different components of the piscivore assemblage. The model examines three scenarios that cover the spectrum of potential impacts of functional groups within the piscivore assemblage, two that accept the evidence for prey switching by minor piscivores presented by Baker and Sheaves (2009) and estimate predation impacts on new recruits during and between recruitment events, and one that rejects the prey switching evidence and examines the general impacts on fish prey based on the more traditional approach that assumes mean estimates of fish consumption adequately indicate the impact of various piscivores.

2. Methods

2.1. Piscivore relative importance model (PRIM)

The model incorporates data on variability in the occurrence, number, type and size of fish prey in the diets of each piscivore functional group, as briefly summarised by Baker and Sheaves (2005, 2009), and relative abundance estimates derived from 2 years of block net sampling an intertidal marsh. Functional groups were defined as individual species, groups of closely related species with similar feeding habits, or, in the case of species that showed strong and predictable ontogenetic shifts in the consumption of fish prey, size classes within species (Baker and Sheaves, 2005). To estimate the relative impacts of each piscivore functional group, PRIM multiplies the proportion of individuals likely to consume fish prey (% frequency of occurrence of fish in the diet) by the relative abundance of that group. This provides an estimate of the number of individuals likely to consume fish prey. This estimate is multiplied by the number of fish prey consumed per individual to provide an estimate of the total number of fish prey consumed by each functional group.

Because our sampling design may have under-represented some types of piscivores (e.g. mobile schooling fish), the potential impacts of three groups that are common in tropical Indo-Pacific estuaries, but did not feature prominently in the block net sampling, were also examined. These were: *Ambassis telkara*, large carangids, and *Platycephalus* spp. (Whitfield and Blaber, 1978a; Blaber et al., 1989; Robertson and Duke, 1990; Baker and Sheaves, 2006; Sheaves, 2006). The model was used to predict the abundance of each of these groups required to equal the predicted impact of the piscivore assemblage sampled on the Blacksoil marsh block net site (see Section 2.6).

2.2. Construction of the PRIM

Each predator taxon was divided into size classes reflecting ontogenetic changes in the consumption of fish prey; including changes in the occurrence, number and type of fish prey in the diet, as well as the minimum size at which piscivory occurred and the maximum size at which new recruits were consumed (see Section 2.4). In this context, each predator size class can be considered a functional group. For example, while flathead, *Platycephalus* spp., are generally considered piscivores (Whitfield and Blaber, 1978a; Salini et al., 1990), each of the size classes of *Platycephalus fuscus* used in the model is functionally different in terms of the predation pressure exerted on fish prey (Baker and Sheaves, 2005); new recruits <20 mm rarely eat fish, small individuals (20–50 mm) occasionally consume small fish prey, medium sized flathead (50–300 mm) consume a moderate amount of a range of fish and may be important predators of new recruits, while larger individuals are primarily piscivorous but rarely prey on new recruits.

For each predator functional group, data were summarised on the frequency of occurrence of fish, total number of fish prey ('total fish') and number of non-pelagic or demersal new recruits ('new recruits') (Appendix 1). Demersal new recruits were defined as small recently settled individuals (≤20 mm) that inhabit the shallow-water nursery. Clupeoids, hemirhamphids and atherinids were not included in calculations of the numbers of new recruits consumed by predators because these groups do not show the same degree of preference for shallow-water habitats exhibited by many of the small and juvenile fishes in these systems (Johnston and Sheaves, 2007). As such, the levels of predation by various piscivores on these pelagic fishes does not represent the impact of those predators on shallow estuarine nursery assemblages composed mainly of demersal species.

2.3. Model scenarios

Three general scenarios of the model were run to examine the range of potential predation impacts of major and minor piscivores on shallow-water nursery assemblages; (1) 'between recruitment events', (2) the average or 'no switching', and (3) 'during recruitment events'. Different sets of values were derived for each of the diet parameters to model predation for each scenario (Table 1). While the evidence for prey switching by minor piscivores to target new recruits is compelling (Baker and Sheaves, 2009), it is not unequivocal. Hence, the 'no switching' scenario rejects the prey switching evidence and follows the more traditional approach that assumes the average frequency of occurrence and average numbers of total fish prey represent the predation impact of both minor and major piscivores throughout space and time. The remaining two scenarios accept the evidence for prey switching and incorporate information on variability in the consumption of fish prey.

Because, by definition, major piscivores prey primarily on fish (Whitfield and Blaber, 1978a), the average occurrence and average number of total fish prey should represent their consumption of

Table 1
Summary of parameter values used to model the impacts of minor and major piscivores under different scenarios. Actual parameter values for each taxon/size class are presented in Appendix 1.

Scenario	Minor		Major	
	% Frequency occurrence	# Fish prey	% Frequency occurrence	# Fish prey
1. Between recruitment	Modal frequency (<av.)	Mean (total)	Mean	Mean (total)
2. No switching	Mean	Mean (total)	Mean	Mean (total)
3. During recruitment	Maximum	Mean (new recruits)	Maximum	(a) Mean and (b) maximum (new recruits)

Author's personal copy

fish at most times, including between recruitment events, and these values were used for the 'between recruitment' scenario (Table 1). Furthermore, the frequency of occurrence of fish in the diet of major piscivores cannot increase greatly in response to a recruitment event, since most individuals usually prey on fish anyway. They may however respond by increasing the number of fish prey consumed per individual predator. Therefore, the maximum occurrence, and both average (scenario 3a) and maximum (scenario 3b) number of new recruits were used to model the impact of major piscivores during recruitment events (Table 1).

In contrast to the overall high level of consumption of fish by major piscivores, minor piscivores appear to feed on alternate prey most of the time while occasionally switching to prey heavily on new recruits (e.g. Martin and Blaber, 1983; Baker and Sheaves, 2009). As a consequence the average occurrence of fish in the diet of minor piscivores would overestimate their impact on prey fish populations at most times (between recruitment events), while occasionally greatly underestimating it (during recruitment events). Therefore, to model the predation impact of minor piscivores, the modal frequency of occurrence (which is less than mean occurrence) and average number of fish prey was used as an estimate of the consumption of fish prey between recruitment events, while the maximum occurrence and average number was used for the 'during recruitment' scenario (Table 1).

2.4. Derivation of model parameters

General summaries of the diet data and statistical techniques used to derive the model parameters are presented in Baker and Sheaves (2005, 2009). Briefly, average frequency of occurrence values were derived from smoothed ontogeny models, or directly from gut content summaries (Baker and Sheaves, 2005). Published dietary data for six species (*A. telkara* [Haywood et al., 1998; Davis, 2001], *Sillago maculata* [Maclean, 1971], *Sillago sihama* [Gunn and Milward, 1985; Wright, 1988; Weerts et al., 1997], *Acanthopagrus berda* [Beumer, 1978; Salini et al., 1990, 1998], *Sphyraena barracuda* [Blaber, 1982], and *Terapon jarbua* [Whitfield and Blaber, 1978b]), provided sufficient detail to allow the combination of the published data with frequency of occurrence data from the current study. This provided average frequency of occurrence values from a larger sample size and with greater spatio-temporal distribution. Maximum occurrences were calculated from the maximum occurrences on individual sampling occasions (Baker and Sheaves, 2009), or from published literature (references above). Average and maximum numbers of total fish prey and new recruits were derived from quantile regressions of predator size – number of prey relationships or taken directly from the raw gut content data (Baker and Sheaves, 2005). The frequency of occurrence and number of fish prey values were based on the smoothed ontogeny models or quantile regressions when there was sufficient data, and the values used for each size class were the predicted values for the size class midpoint.

2.5. Composition of the piscivore assemblage of a high intertidal marsh

Abundance data were collected by block net sampling a high intertidal marsh in Blacksoil Creek (19°18′ S, 147°3′ E, see Baker and Sheaves, 2005 for map of study site) to provide relative abundance estimates to use in the piscivore relative importance model. The block net site was in the lower reach of the Blacksoil Creek estuary, <1 km upstream from the mouth. On a 2.7 m high tide, there is approximately 1 ha of flooded marsh, connected to the main estuary through a ~30 m wide entrance channel with a maximum depth of 1.4 m. The substrate is sand and the marsh is fringed with sparse mangroves (mainly *Rhizophora stylosa* and *Avicennia marina*) and salt cooch (*Sporobolis virginicus*). The block net site is one of several inlets onto a larger marsh complex which combine to form several hectares of flooded marsh on large spring tides (over about 3.0 m).

Sampling was conducted a total of six times during 2003 and 2004. Each year, samples were collected in April (late wet/early dry), August (dry season) and November (early wet). Exact sampling dates were chosen when a high tide of approximately 2.5–2.7 m occurred around 8 am, falling to a low of <1.0 m around 6 h later. Such tides meant that the entire marsh drained completely and remained dry for long enough to complete sampling before the following incoming tide flooded the marsh. The high tide of <2.9 m also ensured the site comprised a single discrete body of water that did not connect to adjacent areas and provide fish with alternate routes back into the subtidal channel of the estuary.

The net (75 × 2 m, 12 mm knotless mesh) was set by hand at slack high water across the entrance of the marsh. The net was hung from PVC poles with the lead line buried in a pre-dug trench and the float line suspended ~50 cm above the waters surface (at high tide) to prevent fish escaping beneath or over the net. As the tide receded, fish were collected from within the enclosed area using cast nets and dip nets. Captured fish were transferred into aerated, flow-through holding tanks and processed in the field. Fish were identified, measured, weighed, and released downstream of the net. Fish that could not be identified or those considered to be in too poor condition for release, were placed on ice and taken to the laboratory for sorting. In the laboratory, the same details were recorded as for the field-processed fish (ID, length, weight). Predatory fishes collected during block net sampling were not retained for gut content analysis because of the potential for in-net predation to bias gut contents (Salini et al., 1998).

2.6. Predicting predation impact of other estuarine piscivores

Because our sampling design may have under-represented some types of piscivores, the potential impacts of three groups of piscivores; *A. telkara*, large carangids, and *Platycephalus* spp. that are common in tropical Indo-Pacific estuaries but did not feature prominently in the block net sampling, were examined.

2.6.1. A. telkara

The model was used to predict the abundance of *A. telkara* on the marsh required; 1) to equal the predicted impact of the major piscivores in the April 2003 sample (highest predicted impact of major piscivores on new recruits); 2) to equal the total impact of all piscivores (major and minor, excluding *A. telkara*) in the November 2003 sample (highest predicted total predation impact on new recruits); and 3) to equal the total impact of major piscivores pooled across all six sampling occasions. For each of these scenarios, the required abundance of *A. telkara* was modelled under the 'during recruitment' scenario (Table 1).

2.6.2. Large carangids

Caranx sexfasciatus >148 mm consumed the greatest average and maximum number of demersal new recruits of all the predators examined by Baker and Sheaves (2005) (Appendix 1). Therefore to examine the relative potential impact of mobile carangids on new recruits, the model was used to estimate the abundance of large (>148 mm) *C. sexfasciatus* required to exert the same predation mortality as the combined minor piscivores in the April 2003 and the November 2003 samples. These dates were chosen as they represent the lowest and highest predicted impacts respectively of minor piscivores on new recruits on the Blacksoil marsh. The required abundance of *C. sexfasciatus* was modelled under the

Author's personal copy

"during recruitment" scenario using both the average and maximum number of new recruits per *C. sexfasciatus* (Table 1; scenario 3a & 3b).

2.6.3. *Platycephalus spp.*

As for *C. sexfasciatus*, the numbers of medium to large flathead, *Platycephalus* spp., required to equal the impact of minor piscivores in the April and November 2003 samples were estimated. The *P. fuscus* 80–300 mm functional group was used as this was the flathead group with the highest observed average and maximum consumption of new recruits (Appendix 1).

3. Results

3.1. Potential responses of different piscivore groups to recruitment events

Within the estuarine piscivore assemblage of north-eastern Australia (Appendix 1), most individuals of the major piscivores in general, and the carangid major piscivores in particular (abbreviated to 'carangids' in this section), prey on fish most of the time. Thus there is little difference between the average and maximum occurrence of fish in their diets (Table 2). The minor piscivores show greater difference between average and maximum frequency of occurrence of fish (Table 2); on average few individuals consume fish prey, but occasionally a large proportion do so.

In contrast to the patterns of variation in the occurrence of fish, the major piscivores show greater variation in the number of fish prey consumed per individual than the minor piscivores (Table 2). In particular, the carangids on average consume far more fish prey than the other piscivores, and occasionally individuals consume a very large number of fish prey. However, this pattern does not transfer to the consumption of new recruits. The minor piscivores and major piscivores excluding carangids show relatively little difference between the average number of total fish prey and the average and maximum number of new recruits (Table 2). This indicates that in general these groups do not respond to recruitment events by increasing the number of fish prey consumed per individual. Individual carangids consume more new recruits than the other piscivores (Table 2). However, the carangids consume a lower maximum number of new recruits than the average number of total fish, suggesting that, overall, carangids also do not respond to recruitment events by switching to consume large numbers of new recruits (Table 2). Although individual piscivore taxa/size classes respond differently to changes in the availability of fish prey (Appendix 1), at the functional level of major and minor piscivores the main response is a change in the proportion of minor piscivores consuming fish prey (Table 2).

3.2. Predation on the Blacksoil Creek marsh

A total of 55 taxa, comprising 19,842 fish (including sharks & rays) 1 squid and 8 mud crabs (*Scylla serrata*), were collected in the 6 Blacksoil marsh samples (Appendix 2). Of these, more than 10,500 individuals belonged to taxa that are piscivorous to some degree. The non-piscivorous fishes were primarily mullet (Mugilidae, $n = 8317$). Almost 3500 potential piscivores were excluded from the model due to insufficient dietary data (Appendix 2b). With the exception of just three individuals (1 *Elops hawaiiensis*, 1 *Negaprion acutidens* and 1 squid), all of those excluded would be considered minor piscivores, comprising mainly atherinids, clupeids, gerreids and leiognathids. Consequently, the model underestimates the impact of the minor piscivores on prey fishes on the Blacksoil marsh.

Among the assemblage of piscivores sampled from the Blacksoil Creek intertidal marsh, the piscivore relative importance model predicts that under all scenarios minor piscivores contribute significantly to the predation mortality of fish on the marsh. Even taking the most conservative view of the potential relative impact of minor piscivores on fish prey, (the 'between recruitment events' scenario, Table 1), minor piscivores were predicted to account for between 10.8% (April 03) and 72.7% (Aug 04) of total predation mortality on the marsh (Table 3). On four of the six sampling occasions, minor piscivores were predicted to consume greater numbers of fish prey than major piscivores. On the occasion with the highest predicted overall predation mortality of juvenile fish under the 'between recruitment events' scenario (Nov 04), minor piscivores were predicted to consume 54.7% of the fish prey eaten (Table 3).

Under the 'no switching' scenario, minor piscivores were predicted to account for between 31.6% (Apr 03) and 89.7% (Aug 03) of predation impact on fish utilising the marsh (Table 3). Once again the Nov 04 sample had the highest predicted overall mortality of fish prey on the Blacksoil marsh, and under the 'no switching' scenario, minor piscivores were predicted to account for 67.3% of this mortality. On five of the six sampling occasions, minor piscivores were predicted to consume more fish prey than major piscivores under the 'no switching' scenario (Table 3).

The 'during recruitment events' scenario predicts that minor piscivores account for between 72.8% (Apr 03) and 99.0% (Aug 04) of the total predation mortality inflicted on new recruits entering the high marsh (Table 3). The Nov 03 sample of piscivores had the highest predicted impact on new recruits on the Blacksoil marsh, and minor piscivores were predicted to account for 96.9% of this impact. When the major piscivore impact was estimated using the maximum occurrence and maximum number of new recruits per individual (Table 1; scenario 3b), the predicted predation impact of minor piscivores still exceed that of the major piscivores on all six sampling occasions, ranging from 50.2% (Apr 03) to 97.0% (Aug 04) of the total predicted impact.

3.3. Relative predation impacts of different functional groups

Overall, minor piscivores featured prominently among the piscivore functional groups predicted to have the greatest predation impacts on the Blacksoil marsh, pooled across all six sampling occasions (Table 4). In fact, under each scenario it was a minor

Table 2
Responses of piscivores to changes in the availability of fish prey, based on the gut contents of 4985 fishes from more than 50 taxa. Parameter values are averaged across all taxa/size classes within the functional group, CV is in parentheses. Parameter values for individual taxa/size classes are presented in Appendix 1.

Piscivore functional group	Parameter					
	% Freq. occurrence		# Total fish		# New recruits	
	av.	max.	av.	max.	av.	max.
Minor	17.2 (0.67)	59.3 (0.44)	1.5 (0.70)	3.0 (1.08)	1.6 (0.75)	2.0 (1.01)
Major excluding carangids	76.9 (0.24)	93.9 (0.13)	1.9 (0.52)	5.6 (1.03)	1.4 (0.67)	2.3 (0.74)
Carangid major piscivores[a]	82.7 (0.18)	96.3 (0.10)	15.7 (1.50)	48.3 (1.36)	7.9 (1.16)	14.5 (1.06)

[a] Data for *M. cordyla* ($n = 1$) excluded from calculations.

Author's personal copy

Table 3
Summary of piscivore relative importance model outputs: predicted impacts of minor and major piscivores on Blacksoil Ck intertidal marsh under the different model scenarios. Number of prey are the predicted number of prey consumed by the piscivore functional group on the marsh. %m:M is the percentage of total consumption by minor (m) and major (M) piscivores. Bold: minor piscivore impact > major piscivore impact.

Date	Scenario											
	Between recruitment events				No switching				During recruitment			
	Number of prey				Number of prey				Number of prey			
	Minor	Major	Total	%m:M	Minor	Major	Total	%m:M	Minor	Major	Total	%m:M
Apr 03	8.7	72.2	80.9	10.8:89.2	33.4	72.2	105.6	31.6:68.4	**286.8**	**107.1**	**393.9**	**72.8:27.2**
Aug 03	**15**	**7.1**	**22.1**	**67.9:32.1**	**61.4**	**7.1**	**68.5**	**89.7:10.3**	**812.2**	**10.4**	**822.6**	**98.7:1.3**
Nov 03	**53.9**	**28.5**	**82.4**	**65.4:34.6**	**141.6**	**28.5**	**170.1**	**83.2:16.8**	**1328.1**	**42.5**	**1370.6**	**96.9:3.1**
Apr 04	29.1	78.1	107.2	27.2:72.8	**78.3**	**78.1**	**156.4**	**50.1:49.9**	**727**	**84.8**	**811.8**	**89.6:10.4**
Aug 04	**11.2**	**4.2**	**15.4**	**72.7:27.3**	**29.3**	**4.2**	**33.5**	**87.4:12.6**	**321**	**3.4**	**324.4**	**99:1**
Nov 04	**72.7**	**60.3**	**133**	**54.7:45.3**	**124**	**60.3**	**184.3**	**67.3:32.7**	**556.9**	**92.8**	**649.7**	**85.7:14.3**
Pooled total	190.7	250.5	441.2	43.2:56.8	**468.1**	**250.5**	**718.6**	**65.1:34.9**	**4031.9**	**340.9**	**4372.8**	**92.2:7.8**

piscivore that was predicted to have the greatest impact of all the piscivore functional groups. Three minor piscivores ranked in the top ten under the 'between recruitment' scenario; *Scomberoides lysan* 20–54 mm (1st), *Sillago analis* (4th) and *Sillago ciliata* (8th). The other piscivore groups predicted to contribute considerable mortality to fish prey on the marsh between recruitment events were major piscivores including *S. lysan* ≥55 mm (2nd), the belonids *Strongylura strongylura* (ranked 3rd) and *Tylosurus crocodilus* (7th), the sphyraenid *S. barracuda* (5th), the platycephalids *P. fuscus* (6th) and *Platycephalus endrachtensis* (10th), and the paralichthyid *Pseudorhombus arsius* >30 mm (9th).

Under the no switching scenario, the minor piscivores *Scomberoides lysandes* <55 mm and *Sillago ciliata* ranked 1st and 2nd respectively among all the piscivore groups (Table 4). Five of the top ten highest ranked piscivore groups were minor piscivores under this scenario, and included *S. analis* (4th), *A. telkara* (6th) and *T. jarbua* (7th). The model predicts that during recruitment events minor piscivores contribute eight of the top ten highest ranking impacts on new recruits (Table 4). *Scomberoides lysan* ≥55 mm and *Strongylura strongylura* are the only major piscivores to rank in the top ten (ranked 7th and 8th), consuming approximately 10% and 5% respectively of the number of new recruits of the highest ranked piscivore, *S. analis*.

Some of the major piscivores (*S. barracuda*, *P. fuscus* ≥50 mm, *P. endrachtensis* ≥50 mm, *Tylosurus gavialoides*), are predicted to consume fewer prey under the 'during recruitment' scenario than under the two more conservative scenarios (Table 4). This is because certain sized individuals in these groups consume few or no new recruits (e.g. *P. fuscus* >300 mm, Baker and Sheaves, 2005). The 'during recruitment' scenario models the impact on new recruits only, while the other scenarios predict the impact on fish prey in general. As such, the 'during recruitment' scenario indicates the new recruit component of the piscivore diet only, not the total amount of fish consumed.

3.4. Predicting predation impact of other estuarine piscivores

Seventy four *A. telkara* (<0.007 ind. m^{-2}) could potentially inflict greater predation pressure on new recruits on the Blacksoil marsh

Table 4
Relative importance of different piscivore functional groups on the Blacksoil marsh, pooled across all samples. Total fish is the predicted total number of fish prey consumed by each group under each scenario Bold: minor piscivore.

Piscivore functional group	Scenario					
	Between recruitment		No switching		During recruitment	
	Rank	Total fish	Rank	Total fish	Rank	Total fish
***Scomberoides lysan* 20–54 mm**	**1**	**121.7**	**1**	**180.1**	**4**	**269**
S. lysan ≥55 mm	2	101.4	3	101.4	7	189.7
Strongylura strongylura ≥40 mm	3	63.8	5	63.8	8	93.6
***Sillago analis* ≥30 mm**	**4**	**32.3**	**4**	**71**	**1**	**1936.2**
Sphyraena barracuda ≥20 mm	5	19.2	8	19.2	16	8
Platycephalus fuscus ≥50 mm	6	16.8	9	16.8	23	1.1
Tylosurus crocodilus ≥40 mm	7	14.8	10	14.8	13	18
***Sillago ciliata* ≥30 mm**	**8**	**13**	**2**	**116.6**	**2**	**666**
Pseudorhombus arsius >30 mm	9	11.5	11	11.5	14	11.5
Platycephalus endrachtensis ≥50 mm	10	10.9	12	10.9	15	9.8
Tylosurus gavialoides ≥40 mm	11	10.2	14	10.2	17	6.5
***Ambassis telkara* >20 mm**	**12**	**7.6**	**6**	**40.2**	**3**	**503.7**
***Gerres filamentosus* >20 mm**	**13**	**7.3**	**15**	**7.3**	**5**	**266.8**
***Terapon jarbua* ≥30 mm**	**14**	**2.4**	**7**	**21.7**	**6**	**253.4**
***Sillago sihama* ≥30 mm**	**15**	**2.4**	**17**	**5.9**	**11**	**28.4**
Psammogobius biocellatus	16	1.9	20	1.9	19	2.8
***Lutjanus fulviflamma* ≥20 mm**	**17**	**1.8**	**19**	**2.3**	**20**	**2.3**
Stolephorus sp. ≥40 mm	18	0.9	13	10.3	12	18.8
***Acanthopagrus berda* >20 mm**	**19**	**0.6**	**16**	**6.3**	**10**	**34.3**
***A. australis* >20 mm**	**20**	**0.5**	**18**	**5**	**9**	**46.5**
***Scomberoides commersonianus* 20–59 mm**	**21**	**0.3**	**21**	**0.9**	**21**	**1.5**
***P. fuscus* 20–49 mm**	**22**	**0.1**	**22**	**0.2**	**22**	**1.1**
***Sillago maculata* ≥30 mm**	**23**	**<0.1**	**23**	**0.2**	**18**	**3.9**
% Total contribution minor:major		**43.2**:56.8		**65.1**:34.9		**92.2**:7.8

Author's personal copy

Table 5
Estimated abundance of selected piscivores needed to equal or exceed the impact of the piscivore assemblage sampled on the Blacksoil marsh. Minor piscivores were modelled under the 'during recruitment' scenario, while major piscivores were modelled under the during recruitment scenario for consumption of both a) average, and b) maximum number of new recruits, as per Table 1. The required abundance is listed as both the number of individuals and the equivalent density (individuals m^{-2}) on the Blacksoil marsh.

For the piscivore group	To equal the impact of	Impact	Required abundance	Equivalent density on Blacksoil marsh
Ambassis telkara	Major piscivores, April 03, scenario 3a	107.1	74	0.0074
	Major piscivores, pooled all samples, scenario 3a	340.9	234	0.0234
	All piscivores, November 03	1156	792	0.0792
	Major piscivores, April 03, scenario 3b	284	195	0.0194
	Major piscivores, pooled all samples, scenario 3b	848.4	582	0.0581
Caranx sexfasciatus >148 mm				
Scenario 3a	Minor piscivores, April 03	286.8	11	0.0011
	Minor piscivores, November 03	1328.1	50	0.0049
Scenario 3b	Minor piscivores, April 03	286.8	7	0.0006
	Minor piscivores, November 03	1328.1	29	0.0028
0.5				
Platycephalus fuscus 80–300 mm				
Scenario 3a	Minor piscivores, April 03	286.8	179	0.0178
	Minor piscivores, November 03	1328.1	826	0.0826
Scenario 3b	Minor piscivores, April 03	286.8	76	0.0076
	Minor piscivores, November 03	1328.1	351	0.0351

than the major piscivores sampled in April 2003 (Table 5). This was the sample with the highest predicted predation pressure by major piscivores under the 'during recruitment' scenario (Table 3). In fact, 234 individuals (0.023 ind. m^{-2}) could consume more new recruits than the predicted total consumption by major piscivores pooled across all six sampling occasions (Table 5). Even if the maximum proportion of major piscivores were to consume the maximum number of new recruits recorded per individual (Table 1; scenario 3b), 195 *A. telkara* (0.02 ind. m^{-2}) modelled under the 'during recruitment' scenario would exceed the impact of the major piscivores sampled in April 2003, while 582 individuals (0.058 ind. m^{-2}) would consume more than all the major piscivores combined. Seven-hundred and ninety-two *A. telkara* (0.079 ind. m^{-2}) could inflict greater mortality on new recruits on the Blacksoil marsh than all of the other piscivores sampled in November 2003 (Table 5), the occasion with the greatest predicted total impact on new recruits (Table 3).

Eleven *C. sexfasciatus* >148 mm would exceed the impact of the minor piscivores in the April 03 sample under the 'during recruitment' scenario (a), while 50 would be needed to exceed the minor piscivore impact from the November 03 sample (Table 5). When the impact of *C. sexfasciatus* was predicted under the 'during recruitment' scenario (b), the required abundances were 7 and 29 respectively. Similarly, 179 and 826 *P. fuscus* 80–300 mm (0.022–0.100 ind. m^{-2}) could consume the same number of new recruits as the minor piscivores sampled in April 03 and November 03 respectively (Table 5). If the maximum proportion of flathead consumed the maximum recorded number of new recruits per individual (during recruitment scenario b), then 76 and 351 individuals (0.008–0.035 ind. m^{-2}) would equal the predation impact of the minor piscivores on the Blacksoil marsh in April and Nov 03.

4. Discussion

Typically, the importance of various piscivores has been implied based on the frequency of occurrence of fish in the diet alone, with only those species with a high occurrence being considered important (e.g. Whitfield and Blaber, 1978a; Blaber, 1980, 1986; Salini et al., 1990, 1998). The piscivore relative importance model expands on this view and provides a more comprehensive measure of the relative predation impact of different members of the piscivore assemblage by combining information on the spatio-temporal and ontogenetic variability in occurrence and composition (identity, size and number) of fish in the diet, and on the relative abundance of the different piscivore taxa.

4.1. Responses of predators to recruitment events

There are a range of responses within the piscivore assemblage to changes in the availability of fish prey, such as occur during recruitment events. At the functional level of major and minor piscivores, the response that has the largest potential impact on new recruits is an increase in the proportion of minor piscivores consuming fish prey (Table 2). The predicted impacts of the minor piscivores increase by approximately an order of magnitude from the 'between recruitment events' to the 'no switching' and from the 'no switching' to the 'during recruitment events' scenarios (Table 3), primarily as a function of an increase in the frequency of occurrence of fish in the diet of these highly abundant predators (Table 2). In contrast, the relatively small changes in the frequency of occurrence of fish prey among the low abundance major piscivores have little effect on the overall predation impact of these predators (Tables 2 and 3).

Major piscivores prey primarily on fish (Whitfield and Blaber, 1978a). Many of those examined during this study include demersal new recruits in their diet (Table 2, Appendix 1), however it seems that few of the major piscivores respond to recruitment events by specifically targeting new recruits. Consuming large numbers of small individual prey may not be an energetically efficient foraging mode for some of these predators (Hughes, 1980). Predator-prey size relationships indicate that ambush predators such as *Platycephalus* spp. and *P. arsius* generally consume relatively large fish prey (Baker and Sheaves, 2005). This may reflect the relative energy returns gained by lunging from ambush cover to capture different sized prey (Hughes, 1980). In contrast, several of the carangids tend to focus predation efforts on prey fish much smaller than the largest fish prey they are capable of eating (Baker and Sheaves, 2005). While *C. sexfasciatus* and *S. lysan* >55 mm do consume large numbers of demersal new recruits, the small prey in the diets of other carangids were mainly pelagic clupeoids. Species such as *Caranx ignobilis* may be more efficient at attacking pelagic fish prey from below rather than attacking demersal new recruits near the substrate from above (Sancho, 2000). Edgar and Shaw (1995) found a similar division in prey types consumed by piscivorous fishes in a southern Australian estuary, with the benthic

Author's personal copy

ambush predators preying mainly on demersal fishes, while the mobile predators preyed heavily on pelagic fish prey. Few individual minor piscivores were found to have consumed more than 1 or 2 fish prey, most of which were new recruits (Table 2, Appendix 1). Despite this, the greatest potential response from within the piscivore assemblage to a recruitment event is a switch by the highly abundant minor piscivores increasing the proportion of individuals consuming fish prey.

4.2. Relative importance of different piscivores on the Blacksoil marsh

The piscivore relative importance model (PRIM) predicts that a range of fishes which on average have a low occurrence of fish in the diet (the minor piscivores) have the greatest impact on new recruits utilising the Blacksoil marsh. Even comparing the most conservative prediction of the potential impact of minor piscivores with the highest predicted impact of major piscivores from the same sample, the minor piscivores would still regularly exert greater predation pressure on fish prey on the Blacksoil marsh (Table 3). It is clear then, that regardless of whether the evidence for prey switching presented by Baker and Sheaves (2009) is accepted or rejected, these previously overlooked piscivores have great potential to contribute significantly to the shaping of tropical estuarine fish faunas and structuring shallow-water nursery assemblages.

Most of the taxa predicted to have the greatest impacts on fish prey on the Blacksoil marsh are widespread and abundant throughout the tropical and subtropical Indo-Pacific (Robertson and Duke, 1987; Blaber and Milton, 1990; Morton, 1990; Blaber, 1999; Sheaves, 2006). For example, 66% of East African estuarine fish species occur in South-East Asian estuaries (Blaber, 1999). Species such as *A. telkara*, *A. berda*, *S. barracuda* and *T. jarbua*, and taxonomically similar species, extend well into subtropical systems in both Australia and southern Africa (e.g. Whitfield and Blaber, 1978b; Blaber, 1982; Morton, 1990). It is likely then that the taxa predicted to be important on the Blacksoil marsh, or their close relatives, are also important predators in shallow estuarine habitats at the broader regional scale.

4.3. Predicting predation impact of other estuarine piscivores

The model provided insight into the potential importance of three groups of piscivores that are common in the regions estuaries but did not occur in large numbers in the Blacksoil samples. *Ambassis telkara* (previously reported as *A. gymnocephalus* or *A. vachelli* in local estuaries, Komori, 2001) is a highly abundant estuarine fish throughout the tropical Indo-West Pacific, often dominating samples in terms of both number and biomass (Martin and Blaber, 1983; Blaber et al., 1985, 1989; Robertson and Duke, 1990; Sheaves, 2006). *Ambassis telkara* shows a strong affinity for shallow-water habitats (Johnston and Sheaves, 2007) and may switch from zooplankton to prey heavily on fish recruiting to estuarine nurseries (Martin and Blaber, 1983; Baker and Sheaves, 2009).

Sheaves (2006) recorded *A. telkara* in shallow sandy habitats in the lower reaches of nine local estuaries (including Blacksoil Creek) at mean ($\pm$1 SE) densities of 0.20 ± 0.05 ind. m^{-2}, and up to a maximum of 11.91 ind. m^{-2}. In the present study, the 147 individuals captured in November 2003 represented the greatest density of these collected during the block net sampling ($\sim$0.0147 ind. m^{-2}). Clearly, the predicted densities of *A. telkara* required to equal the impact of other piscivores on the Blacksoil marsh (0.007–0.079 ind. m^{-2}, Table 5) are well within reasonable probability. It would therefore seem likely that this species would regularly inflict a significant proportion of the total predation mortality on new recruits in shallow estuarine nurseries. Large schools of *A. telkara* could exert massive mortality on new recruits entering the estuary on a single incoming tide (Martin and Blaber, 1983), but detecting such an event by examining gut contents is only possible for a few hours afterwards (Haywood, 1995).

The number of large mobile carangids such as *C. sexfasciatus* required to exceed the impact of the minor piscivores on the Blacksoil marsh may initially seem relatively low (Table 5). However, to place these figures into context it should be noted that the predicted numbers of new recruits consumed per functional group represent the estimated consumption during equal feeding periods (see Section 4.4). Many of the minor piscivores dominate the shallow-water nursery assemblage (Robertson and Duke, 1987, 1990; Sheaves, 2006), and remain in shallow-water habitats most of the time (Johnston and Sheaves, 2007). Larger mobile piscivores such as the carangids appear to only periodically enter these habitats to feed for short periods of time (Blaber et al., 1985; Baker and Sheaves, 2006). The predicted numbers of *C. sexfasciatus* required to match the impact of the minor piscivores represent the number that would need to stay on the marsh feeding for equal time as the 'resident' minor piscivores.

If a group of carangids were to enter the Blacksoil marsh to feed for, say, 10 min on a high tide, there would need to be approximately 220 individuals feeding at the maximum rate recorded for *C. sexfasciatus* to match the minimum predicted impact of minor piscivores that remained on the marsh feeding for 6 h across the high tide. It would take more than 1000 carangids feeding for 10 min to match the maximum predicted impact of minor piscivores on the Blacksoil marsh over one high tide. While the timeframe of 10 min feeding over a 6 h period is somewhat arbitrary in the absence of quantitative data on the periodicity of feeding by mobile piscivores in shallow waters, it provides a prediction that can be tested against field observations. Sampling the Blacksoil marsh on six occasions over 2 years could have significantly underrepresented pulse events such as the ingress of schooling predatory carangids, and alternate approaches such as visual census may help to clarify the impacts of such groups (Baker and Sheaves, 2006).

Large flathead (*Platycephalus* spp. $\geq$100 mm) have been observed in shallow sandy habitats in this region at average densities of 0.043 ind. m^{-2}, and up to 0.197 m^{-2} (Baker and Sheaves, 2006). These densities are equivalent to the predicted required density for flathead to match the impact of minor piscivores on the Blacksoil marsh (Table 5). However, the flathead observed during the visual surveys of Baker and Sheaves (2006) tended to form high density aggregations. It is not clear if the high densities of flathead in narrow strips along the shore would occur at scales such as the area of the Blacksoil marsh, a 1 ha area connected to the main estuary through a narrow entrance channel. What can be inferred, assuming that the Blacksoil marsh sample is generally representative of the shallow-water estuarine fauna (see below), is that the high density aggregations of flathead observed along shallow shorelines (Baker and Sheaves, 2006) potentially exert a significant proportion of the predation pressure on small fishes utilising these habitats. It should be noted, however, that large flathead (*P. fuscus* $>$ 300 mm) rarely consume new recruits (Baker and Sheaves, 2005). Individuals $>$300 mm accounted for almost 40% of the flathead observed during the visual surveys (Baker and Sheaves, 2006). So while these high density aggregations may prey heavily on small fish in the shallow nursery, they are likely to have a lesser impact on the critical early mortality rates of new recruits.

4.4. Model assumptions, interpretation and implications

Ontogenetic dietary changes for many of the piscivore taxa are gradual (e.g. Baker and Sheaves, 2005) and likely to be spatio-temporally variable. As such, the size classes used in the model

Author's personal copy

should be considered as representative of general ontogenetic changes, and as an expedient for modelling the assemblage, rather than as strict boundaries defining precise ontogenetic stages. Two assumptions of the model are that each of the different piscivore functional groups feed for the same length of time each day and digest all fish prey at approximately the same rate, such that the gut contents of any individual predator is directly comparable to that of any other predator.

Digestion rate experiments indicate that several predators, across a range of sizes, digest both fish (*Ambassis*) and crustacean (*Acetes*) prey of various sizes at approximately the same rate, taking around 6 h to completely digest the prey (Baker, 2006). Similar experiments indicate that the clupeid *Herklotsichthys* sp. from the same region digest planktonic crustaceans (*Artemia*) in 6 h (Knott, 2005). The rate of prey digestion is largely controlled by temperature (Weatherly and Gill, 1987), and is thus likely to be relatively constant across predatory fish taxa within any particular environment.

Obviously the 6 samples from the Blacksoil marsh do not represent the entire shallow-water fish fauna from estuaries of the tropical Indo-Pacific, and thus the observed patterns of predation may be specific to this subset of the total shallow-water fauna. The total of 55 taxa sampled from the Blacksoil marsh compares with that of 117 species recorded by Sheaves (2006) from shallow sandy habitats in the lower reaches of 9 estuaries in this region (including Blacksoil Ck), 128 species recorded by Robertson and Duke (1990) from shallow waters of the nearby Alligator Ck estuary, 55 species recorded in Trinity Inlet some 300 km to the north (Blaber, 1980), 197 species recorded by Blaber et al. (1989), who sampled both shallow-water habitats and the open channels of the Embley estuary in far north Queensland, and between 8 and 93 species sampled from 13 estuaries in the Solomon Islands (Blaber and Milton, 1990). While the fishes sampled from the Blacksoil marsh are clearly a subset of the shallow-water estuarine fauna of the tropical Indo-Pacific, the dominant taxa characteristic of such habitats throughout the region, such as mugilids, sillaginids, leiognathids, engraulids, and clupeids (Blaber, 1980; Robertson and Duke, 1987; Blaber et al., 1989; Blaber and Milton, 1990; Sheaves, 2006), also dominated the assemblage sampled in the present study (Appendix 2).

Robertson and Duke (1987) and Sheaves (2006) noted the replacement of particular species by congeners in different estuaries. For example, *S. maculata* was the dominant species of *Sillago* in several estuaries in the region (Sheaves, 2006) but it was sampled in only low abundances on the Blacksoil marsh where *S. analis* and *S. ciliata* dominated. *Sillago maculata* had the highest maximum occurrence (90%) and average (1.4) and maximum (3) number of new recruits of the four *Sillago* spp. found in this regions estuaries (Appendix 1). As such it would potentially be a major predator in other shallow estuarine habitats in the region, just as *S. analis* and *S. ciliata* were important predators on the Blacksoil marsh. So while the species assemblage sampled from the Blacksoil marsh is a subset of the total shallow-water estuarine fauna of the region, it is functionally representative of this fauna.

Some taxa present in the region were not well represented in the model, and other piscivores not examined here may play important roles in the structuring of estuarine fish assemblages. Almost 3500 potential piscivores sampled on the Blacksoil marsh were not included in the model due to insufficient dietary data, and almost all were minor piscivores. The excluded minor piscivores are common components of tropical Indo-Pacific estuarine fauna, being mainly atherinids, clupeids, gerraeids and leiognathids (Blaber, 1980; Robertson and Duke, 1987; Blaber et al., 1989; Blaber and Milton, 1990; Sheaves, 2006). Consequently, the actual predation impact on new recruits by previously overlooked minor piscivores would be far greater than that predicted by the model.

Around the globe there are many estuarine species that are likely to play a similar functional role as the minor piscivores examined in this study. Dominant members of estuarine fish assemblages that incorporate a small amount of fish prey in their diets are reported widely, including fish from estuaries in Europe (e.g. *Pomatoschistus* spp., Hampel and Cattrijsse, 2004; *Clupea harengus*, Maes et al., 2003), southern Africa (Martin and Blaber, 1983), North America (e.g. White perch *Morone americana*, Monteleone and Houde, 1992), the Bahamas (Layman and Silliman, 2002), and temperate Australia (Edgar and Shaw, 1995). The low average occurrences of fish in the diets of these predators quite possibly reflects a switch to target periodically available new recruits (Martin and Blaber, 1983; Monteleone and Houde, 1992; Baker and Sheaves, 2009). As a consequence, these easily overlooked minor piscivores around the globe may play an important role in structuring estuarine fish assemblages through predation on new recruits.

Even with this clearer picture of the relative importance of different functional groups within the diverse tropical estuarine piscivore assemblage, aspects of the role that predation on new recruits plays in structuring these communities may have still been missed. Some of the piscivores that were not very important on the Blacksoil marsh (e.g. larger carangids, planktivorous clupeoids) may respond to recruitment events by focusing predation on new recruits before they enter the shallow-water nurseries. For example, new recruits may be targeted in open channels as they enter the estuary on an incoming tide by predators that may not prey heavily on them once they reach the shallow nursery. However, different susceptibilities to various sampling gears makes comparably quantifying the relative abundance of mobile fishes in open waters and more sedentary fishes in shallow waters a particularly challenging task (Rozas and Minello, 1997). Further work using some novel approaches is required to quantify the abundance and movement patterns of mobile predators and their potential impacts on recruiting fish in other habitats.

5. Conclusions

Within the shallow nursery, a brief switch by the highly abundant minor piscivores could exert massive mortality on new recruits. A large proportion of the shallow-water fish fauna are potential predators, and occasional intense predation events by largely overlooked minor piscivores have the potential to contribute the majority of predation pressure experienced by the critical early life stages of fishes recruiting to tropical estuaries. Pulse events of processes such as predation or competition are very difficult to detect using standard sampling techniques designed to represent the average levels of a process (Edwards et al., 1982), however such events can have a major influence on observed patterns within these systems (e.g. Köster and Möllmann, 2000; Webster, 2002). Despite the presence of an abundant and diverse piscivore assemblage, the occupation of shallow-water habitats may still provide new recruits with a survival advantage over the occupation of alternate deeper waters (see discussion in Baker and Sheaves, 2007). However, the paradigm that shallow-water habitats within estuaries provide juvenile nekton with refuge from predation appears overly simplistic for diverse systems in tropical Australia as it fails to incorporate dynamic predator–prey interactions at a range of spatial, temporal and ontogenetic scales.

Acknowledgements

This research was supported by a Coastal CRC PhD scholarship to RB. An enormous team of field volunteers assisted in collecting the data presented in this ms, special thanks go to the Estuarine & Coastal Ecology Group, JCU. Two anonymous reviewers provided comments that improved this manuscript. Field sampling was conducted under JCU Ethics approval A621_00.

Author's personal copy

Appendix. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecss.2009.10.006.

References

Baker, R., 2006. Piscivory and the functioning of shallow tropical estuarine nursery grounds. Ph.D. dissertation, James Cook University, Townsville Australia.

Baker, R., Sheaves, M., 2005. Redefining the piscivore assemblage of shallow estuarine nursery habitats. Marine Ecology Progress Series 291, 197–213.

Baker, R., Sheaves, M., 2006. Visual surveys reveal high densities of large piscivores in shallow estuarine nurseries. Marine Ecology Progress Series 323, 75–82.

Baker, R., Sheaves, M., 2007. Shallow-water refuge paradigm: conflicting evidence from tethering experiments in a tropical estuary. Marine Ecology Progress Series 349, 13–22.

Baker, R., Sheaves, M., 2009. Refugees or ravenous predators: detecting predation on new recruits to tropical estuarine nurseries. Wetlands Ecology and Management 17, 317–330.

Beumer, J.P., 1978. Feeding ecology of four fishes from a mangrove creek in north Queensland, Australia. Journal of Fish Biology 12, 475–490.

Blaber, S.J.M., 1980. Fish of the Trinity Inlet system of north Queensland with notes on the ecology of fish faunas of tropical Indo-Pacific estuaries. Australian Journal of Marine and Freshwater Research 31, 137–146.

Blaber, S.J.M., 1982. The ecology of *Sphyraena barracuda* (Osteichthyes: Perciformes) in the Kosi system with notes on the Sphyraenidae of other Natal estuaries. South African Journal of Zoology 17, 171–176.

Blaber, S.J.M., 1986. Feeding selectivity of a guild of piscivorous fish in mangrove areas of north-west Australia. Australian Journal of Marine and Freshwater Researh 37, 329–336.

Blaber, S.J.M., 1999. Assessment of biodiversity, threats, trends and emerging issues: estuarine ecosystems. In: Vidy, G., Albaret, J.J., Baran, E. (Eds.). IRD, Montpellier (France).

Blaber, S.J.M., Milton, D.A., 1990. Species composition, community structure and zoogeography of fishes of mangrove estuaries in the Solomon Islands. Marine Biology 105, 259–267.

Blaber, S.J.M., Young, J.W., Dunning, M.C., 1985. Community structure and zoogeographic affinities of the coastal fishes of the Dampier region of north-western Australia. Australian Journal of Marine and Freshwater Research 36, 247–266.

Blaber, S.J.M., Brewer, D.T., Salini, J.P., 1989. Species composition and biomasses of fishes in different habitats of a tropical northern Australian estuary: their occurrence in the adjoining sea and estuarine dependence. Estuarine Coastal and Shelf Science 29, 509–531.

Boesch, D., Turner, R.E., 1984. Dependence of fishery species on salt marshes: the role of food and refuge. Estuaries 7, 460–468.

Davis, I.L., 2001. Fish and benthic prey distribution and abundance in response to reduced freshwater inflow associated with the end of the wet season, in Ross River estuary, Townsville. Honours thesis, James Cook University, Townsville.

Deegan, L.A., Hughes, J.E., Rountree, R.A., 2000. Salt marsh ecosystem support of marine transient species. In: Weinstein, M.P., Kreeger, D.A. (Eds.), Concepts and Controversies in Tidal Marsh Ecology. Kluwer Academic Publishers, Dorecht.

Edgar, G.J., Shaw, C., 1995. The production and trophic ecology of shallow-water fish assemblages in southern Australia. 2. Diets of fishes and trophic relationships between fishes and benthos at Western Port, Victoria. Journal of Experimental Marine Biology Ecology 194, 83–106.

Edwards, D.C., Conover, D.O., Sutton, F., 1982. Mobile predators and the structure of marine intertidal communities. Ecology 63, 1175–1180.

Gunn, J.S., Milward, N.E., 1985. The food, feeding habits and feeding structures of the whiting species *Sillago sihama* (Forsskal) and *Sillago analis* (Whitley) from Townsville, north Queensland, Australia. Journal of Fish Biology 26, 411–427.

Hampel, H., Cattrijsse, A., 2004. Temporal variation in feeding rhythms in a tidal marsh population of the common goby *Pomatoschistus microps* (Kroyer 1838). Aquatic Sciences 66, 315–326.

Haywood, M.D.E., 1995. Rates at which post-larval prawns are digested by a small predatory fish and the implications for dietary studies. Journal of Fish Biology 47, 337–340.

Haywood, M.D.E., Heales, D.S., Kenyon, R.A., Loneragan, N.R., Vance, D.J., 1998. Predation of juvenile tiger prawns in a tropical Australian estuary. Marine Ecology Progress Series 162, 201–214.

Hughes, R.N., 1980. Optimal foraging theory in the marine context. Oceanography and Marine Biology, Annual Review 18, 423–481.

Johnston, R., Sheaves, M., 2007. Small fish and crustaceans demonstrate a preference for particular small-scale habitats when mangrove forests are not accessible. Journal of Experimental Marine Biology and Ecology 353, 164–179.

Knott, M.J., 2005. Feeding ecology, distribution and composition of zooplanktivorous fish in tropical estuaries. B.Sc. Honours thesis, James Cook University, Townsville.

Komori, K., 2001. Glassfishes (Ambassidae) of Australia and Papua New Guinea: a morphological and molecular approach to species identification and zoogeography. Ph.D. dissertation, Macquarie University, Sydney, NSW.

Köster, F.W., Möllmann, C., 2000. Trophodynamic control by clupeid predators on recruitment success in Baltic cod? ICES Journal of Marine Science 57, 310–323.

Layman, C.A., Silliman, B.R., 2002. Preliminary survey and diet analysis of juvenile fishes of an estuarine creek on Andros Island, Bahamas. Bulletin of Marine Science 70, 199–210.

Levin, P., Stunz, G., 2005. Habitat triage for exploited fishes: can we identify essential "Essential Fish Habitat"? Estuarine Coastal and Shelf Science 64, 70–78.

Maclean, J.L., 1971. The food and feeding of winter whiting (*Sillago maculata* Quoy and Gaimard) in Moreton Bay. Proceedings of the Linnean Society of New South Wales 96, 87–92.

Maes, J., Brabandere, L., Ollevier, F., Mees, J., 2003. The diet and consumption of dominant fish species in the upper Scheldt estuary, Belgium. Journal of the Marine Biological Association of the United Kingdom 83, 603–612.

Martin, T.J., Blaber, S.J.M., 1983. The feeding ecology of Ambassidae (Osteichthyes: Perciformes) in Natal estuaries. South African Journal of Zoology 18, 353–362.

Monteleone, D.M., Houde, E.D., 1992. Vulnerability of striped bass *Morone saxatilis* (Waldbaum) eggs and larvae to predation by juvenile white perch *Morone americana* (Gmelin). Journal of Experimental Marine Biology and Ecology 158, 93–104.

Morton, R.M., 1990. Community structure, density and standing crop of fishes in a subtropical Australian mangrove area. Marine Biology 105, 385–394.

Paterson, A.W., Whitfield, A.K., 2000. Do shallow-water habitats function as refugia for juvenile fishes? Estuarine Coastal and Shelf Science 51, 359–364.

Robertson, A.I., Duke, N.C., 1987. Mangroves as nursery sites: comparisons of the abundance and species composition of fish and crustaceans in mangroves and other nearshore habitats in tropical Australia. Marine Biology 96, 193–205.

Robertson, A.I., Duke, N.C., 1990. Mangrove fish-communities in tropical Queensland, Australia: spatial and temporal patterns in densities, biomass and community structure. Marine Biology 104, 369–379.

Rozas, L.P., Minello, T.J., 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.

Salini, J.P., Blaber, S.J.M., Brewer, D.T., 1990. Diets of piscivorous fishes in a tropical Australian estuary, with special reference to predation on penaeid prawns. Marine Biology 105, 363–374.

Salini, J.P., Brewer, D.T., Blaber, S.J.M., 1998. Dietary studies on the predatory fishes of the Norman River Estuary, with particular reference to penaeid prawns. Estuarine Coastal and Shelf Science 46, 837–847.

Sancho, G., 2000. Predatory behaviors of *Caranx melampygus* (Carangidae) feeding on spawning reef fishes: a novel ambushing strategy. Bulletin of Marine Science 2, 487–496.

Sheaves, M., 2001. Are there really few piscivorous fishes in shallow estuarine habitats? Marine Ecology Progress Series 222, 279–290.

Sheaves, M., 2006. Scale dependent variation in composition of fish fauna among sandy tropical estuarine embayments. Marine Ecology Progress Series 310, 173–184.

Weatherly, A.H., Gill, H.S., 1987. The Biology of Fish Growth. Academic Press, London.

Webster, M.I., 2002. Role of predators in the early post-settlement demography of coral reef fishes. Oecologia 131, 52–60.

Weerts, S.P., Cyrus, D.P., Forbes, A.T., 1997. The diet of juvenile *Sillago sihama* (Forsskal, 1775) from three estuarine systems in KwaZulu-Natal. Water (South Africa) 23, 95–100.

Whitfield, A.K., Blaber, S.J.M., 1978a. Food and feeding ecology of piscivorous fishes at Lake St Lucia, Zululand. Journal of Fish Biology 13, 675–691.

Whitfield, A.K., Blaber, S.J.M., 1978b. Scale-eating habits of the marine teleost *Terapon jarbua* (Forskal). Journal of Fish Biology 12, 61–70.

Wright, J.M., 1988. Recruitment patterns and trophic relationships of fish in Sulaibikhat Bay, Kuwait. Journal of Fish Biology 33, 671–687.