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Piscivory and the functioning of shallow tropical estuarine nursery grounds

Thesis submitted by

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in the Department of Marine Biology and Aquaculture
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Abstract

Shallow estuarine habitats around the world are considered important nurseries for a diverse range of fish and crustaceans of ecological and economic importance. One of the key features believed to contribute to the nursery value of these habitats is that they contain few predatory fishes, and thus provide juveniles with a refuge from predation. Despite its global application, there is very little direct evidence to support the shallow-water refuge paradigm.

Within tropical estuarine systems our current knowledge of the role predation may play in structuring juvenile fish faunas and the functioning of shallow water nurseries is limited to broad summaries of the general dietary habits of a limited range of large piscivorous fishes. Small and occasional or 'minor' piscivores, those predators which on average have a low occurrence of fish in their diet, have largely been ignored. Additionally, there is a lack of quantitative detail on dietary composition and on spatial and temporal patterns in the consumption of fish prey. Such details are needed to clarify the importance of predation on particularly vulnerable or critical life stages such as new recruits. Understanding the processes that drive systems such as estuarine nurseries is critical for the effective management and protection of these important systems into the future. The goal of this thesis is to gain a clearer insight into the role of piscivory within shallow tropical estuarine nursery grounds, and by doing so, to significantly enhance our understanding of the functioning of these important systems.

To define the assemblage of piscivorous fishes relevant to the functioning of shallow water nurseries, the diets of almost 5000 predatory fishes collected over 6 years from shallow (<1.5m) sandy habitats in the lower reaches of 17 tropical estuaries were examined. The piscivore assemblage was diverse in terms of taxonomic composition, size structure and predation strategies. Fifty-one taxa were found to have fed on fish, and the piscivore assemblage included many taxa and size classes that have been previously overlooked. The majority of taxa were piscivorous to some degree from sizes well below 100 mm. All of the smaller piscivores (<100 mm) preyed mainly on small new recruits. The larger more widely recognised piscivores preyed on a broader range of fish prey, however few of these consumed significant numbers of small new recruits. The suggestion that shallow-waters in tropical estuaries contain few piscivorous fishes fails to recognise the potential importance of the abundant and diverse assemblage of small and minor piscivores that utilise these habitats.

The potential importance of previously overlooked occasional or minor piscivores as predators of new recruits was explored by relating recruit abundance to predator diets, and by examining spatial and temporal patterns in the consumption of fish prey. The high spatial patchiness of new recruits made it difficult to correlate their abundance with their consumption by minor piscivores. However, the low average occurrence of fish in the diet of minor piscivores was a poor reflection of the spatial and temporal patterns in predation pressure by these on new recruits to shallow nursery habitats. Most of the time, minor piscivores did not consume fish prey but occasionally a large proportion of them did so. When minor piscivores consumed fish prey, they preyed mainly on small new recruits. Small new recruits were only occasionally abundant, with temporally patchy recruitment to shallow estuarine nurseries. Thus, the low average occurrence of fish in the diet of minor piscivores suggests that while these predators may derive little of their nutritional requirements from fish prey, they may switch to heavily target new recruits. Given that many of the minor piscivores are highly abundant and are themselves small juvenile fishes occupying the shallow nursery habitats, they are potentially major sources of mortality for fish recruiting to shallow estuarine nurseries.

The abundance of large (≥100 mm TL) piscivorous fishes in shallow water habitats where they appeared to have previously been underestimated was determined by visual census. Although flathead (*Platycephalus* spp., Platycephalidae) were the only large piscivores sighted within the transects, the density observed (0.04 ind. m^{-2}) equated to one piscivore for every 10.5 m of shoreline surveyed. This exceeds density estimates for large piscivores in shallow estuarine habitats elsewhere in the world by orders of magnitude. Furthermore, the estimated biomass of flathead (11.56 g m^{-2}) was equivalent to comparable biomass estimates of entire fish assemblages from shallow estuarine habitats in other parts of the world. The densities and depth distribution of these large piscivores, combined with the diverse and abundant assemblage of small and occasional piscivores, suggests that shallow water nurseries may not provide small fishes with the level of refuge from predation previously assumed.

The hypothesis that predation pressure on small fishes is lower in shallow waters than in adjacent deeper water was directly tested by a series of tethering experiments. Over 6 months 17 replicate experimental trials were conducted, deploying a total of 183 tethered fish prey across a depth gradient (0.2 – 3 m) in the lower reaches of a tropical estuary. Despite the clear and consistent patterns found in previous studies elsewhere in the world, there was no evidence of lower predation pressure in the shallow relative to the adjacent deeper waters in the tropical estuaries examined. Given the complexity and diversity of the piscivore assemblage in these estuaries it is hardly surprising that no clear patterns emerged. The findings suggest that the shallow-water refuge paradigm may be too simplistic for diverse and complex tropical estuarine nursery grounds.

Finally, a model was constructed to estimate the relative importance of different members of the diverse shallow water piscivore assemblage within tropical estuaries. 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 gained from block-net sampling an intertidal marsh over 2 years. The model predicts that previously overlooked small and occasional piscivores have the potential to have orders of magnitude greater impacts than more conspicuous larger piscivores on new recruits utilising shallow tropical estuarine habitats as nurseries. Because of their sheer abundance, a switch by the minor piscivores to target new recruits results in a massive increase in the consumption of fish prey by the piscivore assemblage. As a broad functional group, minor piscivores occur in many systems around the globe, and are likely to play important roles in these systems as predators that shape communities by targeting the critical early life stages of other fishes.

This study revealed a diverse assemblage of piscivores with the potential to cause significant mortality on new recruits to shallow water habitats. Many of the piscivores with the greatest potential to shape community structure through predation on new recruits are themselves small juvenile fishes utilising shallow water habitats as nurseries. In contrast to the idea that shallow waters provide refuge from predation, heavy predation on new recruits entering the nursery may represent a significant input of energy and nutrients from coastal waters to estuarine systems and may act to enhance the productivity and hence the nursery ground value of these systems.

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Chapter 1

General Introduction

Located at the interface of land and sea, throughout the world estuaries occur alongside the greatest densities of human populations (Edgar et al. 2000). Estuarine systems are believed to be the most economically valuable aquatic environment per unit area on the planet (Costanza et al. 1997). For example, it has been estimated that 75 % of Queensland's commercial fishery landings are of species reliant on estuarine habitats during some part of their lifecycle (Quinn 1992). These systems upon which we so heavily rely for a range of goods and services are the systems that experience some the greatest direct impacts from human activities (Hutchings & Saenger 1987, Blaber 1999, Alongi 2002, Blaber 2002). Only with a clear understanding of the processes and mechanisms that contribute to the value of estuaries can we hope to effectively manage and protect these systems into the future (Ronnback 1999, Beck et al 2001).

One of the values used to justify the conservation and protection of estuaries around the world is that estuaries in general, and shallow estuarine habitats in particular, are considered critical nurseries for a range of fishes and crustaceans of ecological, cultural and economic importance (e.g. Boesch & Turner 1984, Miller et al. 1985, Robertson & Duke 1987, Robertson 1988, Quinn 1992, Sheaves 1995, Paterson & Whitfield 1996, Beck et al. 2001). A valuable nursery can be defined as such if it provides a greater contribution to the reproduction of the next generation of a species than alternate less-valuable nurseries. This can be achieved by producing larger more fecund individuals, and or by contributing more individuals to the reproductive population, than alternate nurseries. These ideas form the basis of the two fundamental paradigms in estuarine nursery ground ecology; that a valuable nursery should provide high food availability (leading to faster growth and hence greater lifetime fecundity) and/or refuge from predation (resulting in more individuals surviving to reach sexual maturity) (e.g. Blaber & Blaber 1980, Russell & Garrett 1983, Boesch & Turner 1984, Miller et al. 1985, Robertson & Duke 1987, Paterson & Whitfield 2000).

The shallow water refuge paradigm is based, in part, on the apparent low numbers of predatory fishes within shallow estuarine habitats (eg. Shenker & Dean 1979, Rozas & Hackney 1983, Boesch & Turner 1984, Patterson & Whitfield 2000). While structural complexity may alter the relative refuge value provided by various shallow water habitats, the refuge paradigm has been applied across a range of habitat types around the world (Blaber & Blaber 1980, McIvor & Odum 1988, Rozas & Odum 1988, Ruiz et al. 1993, Clark et al. 2003), despite geographic differences in faunal compositions (Blaber 2000), diversity of piscivores (Hartman & Brandt 1995, Blaber et al. 1989), and structural features of the range of habitats (Kneib 1997, Sheaves 2005, Smith & Hindell 2005). Consequently, the shallow water refuge paradigm applies to shallow water habitats per se, regardless of the level of structural complexity (Ruiz et al. 1993).

The utilisation of shallow water habitats by juvenile fishes appears to be a global phenomenon (Shenker & Dean 1979, Boesch & Turner 1984, Robertson & Duke 1987, Ruiz et al. 1993, Paterson & Whitfield 1996, Barletta et al. 2003, Krumme et al. 2004). However, despite the logical basis of the nursery ground paradigms, there is little direct evidence as to the relative importance of food and refuge in shallow water habitats (cf. Miltner et al. 1995, Halpin 2000), nor of the benefits of the use of shallow estuarine over alternate habitats (Sheaves 2001, Rountree & Able 2006). The difficulty in comparatively sampling different habitats may be largely responsible for the paucity of direct assessments of nursery ground value (Boesch & Turner 1984, Kneib 1997, Rozas & Minello 1997, Rountree & Able 2006). Despite the difficulty of unequivocally demonstrating the relative value of shallow estuarine habitats, the mounting evidence suggests that these are indeed important nurseries for many species of fishes and crustaceans (Beck et al. 2001).

The potential refuge value of shallow estuarine nurseries for fishes has usually been inferred indirectly from patterns of habitat use by juveniles and/or piscivores (Cain & Dean 1976, Blaber 1980, Blaber & Blaber 1980, Robertson & Duke 1987, Paterson & Whitfield 2000). Observations of high densities of small juveniles and low numbers of large, primarily piscivorous fishes in shallow habitats has led to the conclusion that predation pressure is lower in shallow than in adjacent deeper waters and thus that shallow waters provide refuge for small fishes (Cain & Dean 1976, Shenker & Dean 1979, Blaber 1980, Blaber & Blaber 1980, Boesch & Turner 1984, Rozas & Hackney 1984, McIvor & Odum 1988, Deegan 1990, Ruiz et al. 1993, Ronnback et al. 1999, Paterson & Whitfield 2000). Recently the proposition that shallow estuarine waters contain few piscivores has come under question, and the role of predation on fishes within shallow estuarine nurseries remains unclear (Deegan et al. 2000, Sheaves 2001, Minello et al. 2003, Rountree & Able 2006).

From a basic survey of the fish fauna of Trinity Inlet at Cairns in north-eastern Queensland, Australia, Blaber (1980) suggested that tropical estuaries contained fewer large piscivorous fishes than adjacent coastal waters and that therefore estuaries provide refuge for juvenile fishes. Although the data on which this proposition was based was limited (Blaber 1980), it aligned with general beliefs about how nurseries *should* function (Cain & Dean 1976, Shenker & Dean 1979, Boesch & Turner 1984). However, this and many other studies have made some critical, and rarely tested, assumptions.

Perhaps because large predatory fishes are capable of consuming large numbers of small fish prey (Blaber 1980), it is generally assumed that only large fishes are potentially important predators (e.g. Cain & Dean 1976, Shenker & Dean 1979, Blaber 1980, Salini et al. 1990, Paterson & Whitfield 2000). Small piscivores have been largely overlooked, or explicitly assumed to be unimportant (Blaber 1980), despite the fact that fishes can be piscivorous from very small sizes (e.g. Blaber 1982). For example, in one of the few direct tests of the hypothesis that shallow waters contain few piscivorous fishes, Paterson & Whitfield (2000) sampled several habitats across a depth gradient using 100 mm mesh gill nets. By using such gear, they were specifically limiting their consideration to large fishes only. However, the combination of individual growth, cohort survival, and individual metabolic rate mean that it is the juvenile stage of a cohort that consume the greatest biomass of prey (Yanez-Arancibia et al. 1994). Thus, although an individual large piscivore can consume more fish prey than a smaller individual, small piscivores as a group will consume more prey than their larger counterparts.

Similarly, the potential importance of occasional or ‘minor’ piscivores (Whitfield & Blaber 1978a) has received little attention (but see Martin & Blaber 1983). It has been assumed that the low average occurrence of fish in the diets of minor piscivores reflects the level of impact of these on fish prey (e.g. Whitfield & Blaber 1978a, Blaber 1980, Salini et al. 1990, 1998). While it may seem superficially reasonable that a species for which fish is the dominant prey type (a primary or major piscivore) is likely to be more important than a species which rarely consumes fish (a minor piscivore), this is a narrow view which again only considers the potential impacts of the individual, and not the impacts of the group at an assemblage or community level. Factors such as the abundance of different predator groups, and spatial and temporal variability in dietary habits may have considerable influence on the structure of predation pressure from different piscivores (Martin & Blaber 1983).

Finally, while the refuge paradigm appears to have been broadly applied to all small and juvenile fishes (e.g. Blaber & Blaber 1980, Boesch & Turner 1984, McIvor & Odum 1988, Ruiz et al. 1993, Rozas & Minello 1998, Paterson & Whitfield 2000), the potential benefits of gaining refuge are likely to change considerably among different life-stages, including during the period of estuarine residency (Yanez-Arancibia et al. 1994, Sogard 1997). Early juvenile stages of fishes suffer very high levels of mortality (Carr & Hixon 1995, Sogard 1997), and small changes in early mortality rates can have a profound influence on ultimate cohort strength (Yanez-Arancibia et al. 1994). An intense pulse of predation on early life stages can play a major role in cohort survivorship and in structuring fish assemblages in other systems such as coral reefs (e.g. Carr & Hixon 1995, Hixon & Carr 1997, Webster 2002, Almany 2004) and pelagic waters (e.g. Ellis & Nash 1997, Köster & Möllmann 2000, Swain & Sinclair 2000). Predation on new recruits to tropical estuarine systems potentially creates a similar ecological bottleneck critical in structuring estuarine fish assemblages and in the functioning of shallow-water nurseries (Martin & Blaber 1983, Halpern 2004, Sheaves 2005).

Twenty-five years on from the early work of Blaber (1980) our understanding of the dynamics of piscivory in the functioning of tropical estuarine systems has advanced little. Information on piscivory within these systems remains limited to a few studies on the general dietary habits of mainly large predatory fishes (Blaber 1986, Salini et al. 1990, 1998, Haywood et al. 1998, Sheaves & Molony 2000). The importance of piscivory in the functioning of these systems was rarely a significant focus of such studies.

In addition to the limited range of species and size classes examined, dietary data on tropical/subtropical estuarine fishes are usually presented pooled over sampling occasions and locations to provide average diets (e.g. Blaber & Blaber 1980, Salini et al. 1990, Haywood et al. 1998, Salini et al. 1998). There is also a lack of quantitative detail on the composition of the fish component of the diet. By pooling dietary data, information on spatial and temporal variability in diets is lost and the potential importance of predators which may occasionally switch to target critical life stages has been overlooked. Finally, even within the recognised piscivore assemblage, the extent of shallow water habitat use by several groups may have been underestimated due to sampling biases (e.g. Blaber et al. 1985, Rountree & Able 1997) because many gears typically used to sample fishes from shallow water habitats may be inefficient at capturing larger, more mobile individuals (Kneib 1997, Rozas & Minello 1997). Consequently, the range of predators that may prey on critical early life stages of fishes within shallow estuarine nurseries, and the role of piscivory in the functioning of these nurseries remains unclear. The goal of this thesis is to gain a clearer insight into the role of piscivory within shallow tropical estuarine nursery grounds, and by doing so, to significantly enhance our understanding of the functioning of these important systems.

To achieve this goal, a number of specific aims will be addressed:

- to gain an understanding of the range of piscivorous fishes that prey on newly recruited fish in shallow tropical estuarine nursery habitats (Chapter 3),
- to examine the potential for minor or occasional piscivores to switch to target new recruits (Chapter 4),
- to determine the abundance of large piscivores in shallow water habitats where they may have previously been underestimated (Chapter 5),
- to directly assess if shallow waters provide small fishes with a refuge from predation (Chapter 6), and
- to estimate the relative importance of different members of the diverse tropical estuarine piscivore assemblage in structuring shallow water fish faunas (Chapter 7).

Chapter 2

Gut content analysis methods and interpretation

Much of the data in this thesis is based on gut content analysis. Many methods for quantifying gut contents of predatory estuarine and coastal fishes have been employed previously, ranging from simple presence/absence or frequency of occurrence (Sheaves & Molony 2000) to estimates of nutritional contribution of each prey type (Hartman & Brandt 1995). For a detailed description of the available techniques, see reviews by Hynes (1950) and Hyslop (1980). This chapter justifies the use of frequency of occurrence data by showing it is the most precise, objective and interpretable method to quantify general dietary composition of the predatory fishes examined in this study.

2.1 Quantifying gut contents. Throughout this thesis the general composition of predator diets is based on frequency of occurrence data of prey in the stomachs, that is, the proportion of individuals in a taxon or size class that contained a particular prey type. The frequency of occurrence technique relies simply on the positive identification of some body part of the prey to provide accurate and precise data on the dietary composition. The relative importance of various prey types is then inferred from the proportion of total guts containing each prey type.

Hyslop (1980) considered that presence/absence or frequency of occurrence provides only a crude qualitative indication of dietary composition because it lacks information on the relative bulk of each prey type. This assessment appears to have been widely adopted and many authors employ or recommend apparently more quantitative techniques such as measuring contribution of each prey type by weight or volume (e.g. Blaber 1986, Salini et al. 1990, Cortes 1997, Haywood et al. 1998, Salini et al. 1998, Liao et al. 2001, Schafer et al 2002). Peers and reviewers of manuscripts and conference presentations regularly express similar sentiments (pers. obs.). Additionally, compound indices incorporating several measures including volume or weight have been proposed to provide a more balanced representation of dietary importance (Liao *et al*. 2001) and to provide standardised methods for reporting fish diets (e.g. Pinkas *et al*. 1971, Mohan & Sankaran 1988, Cortes 1997).

In quantifying gut contents during this study I encountered a serious limitation that compromised any technique that required the physical separation of prey types (e.g. measuring volume or weight); separation could not be done unambiguously and therefore introduced considerable and unquantifiable errors. This is because these techniques assume it is possible to accurately separate individual prey items or prey categories. Partially digested prey remains and loose tissue in the stomach (e.g. Fig. 2.1) cannot be allocated to any prey category with absolute confidence (Schafer et al 2002). This is because it may be the remains of a separate prey item no longer represented by identifiable parts or an inseparable mixture of tissue from multiple prey items. Consequently, loose tissue allocated to any category other than “unidentified” potentially adds error to each volume or weight value obtained, meaning the summarised dietary composition will contain considerable and unmeasurable error.

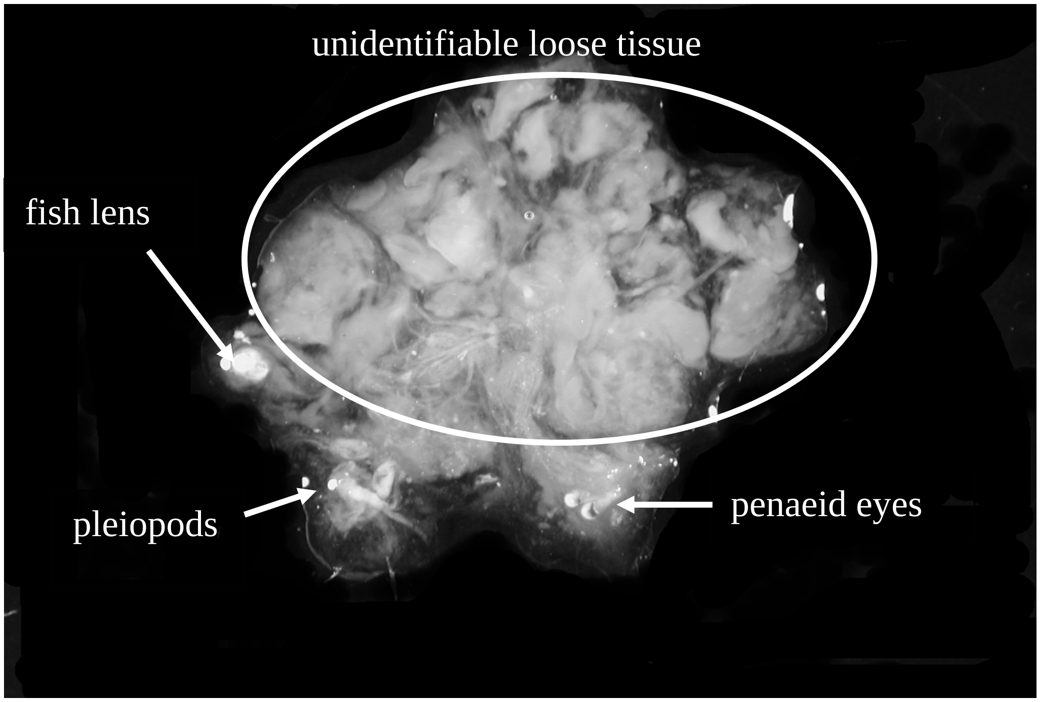


Figure 2.1: Typical prey remains from the gut of a predatory fish, *Scomberoides commersonianus* 349 mm FL.

The level of digestion of prey will determine the difficulty in accurately separating prey types. Sampling gears such as gill nets, widely used in tropical estuarine and coastal dietary studies (e.g. Salini et al. 1990, Blaber et al. 1994, Brewer et al. 1995, Haywood et al. 1998, Salini et al. 1998), often provide guts with highly digested prey because of post-capture digestion of gut contents during the period between capture and retrieval of the gear (Haywood 1995). In the present study the majority of fish were collected by techniques such as seine nets and angling with artificial lures, with captured fish placed immediately in an ice slurry to halt the digestion process, and frozen as soon as possible. Despite this process, less than 5% of individual guts contained intact, easily separable prey items with no free tissue (Table 2.1).

Table 2.1: Percentage of stomachs of predatory tropical estuarine fishes containing different numbers of prey categories, with or without loose unidentifiable tissue (n = 1889 stomachs). For definitions of prey categories, see chapter 3.3.

	Number of identifiable prey categories						
Unidentifiable tissue	**1**	**2**	**3**	**4**	**5**	**6**	total
present	72.4	19.2	3.1	0.4	0.1	0.1	**95.3**
absent	3.8	0.8	0.2	0	0	0	**4.7**

Dietary studies of tropical estuarine and coastal fishes typically record very low proportions of unidentifiable food items (e.g. Salini et al. 1990, Blaber et al. 1994, Brewer et al. 1995, Haywood et al. 1998, Salini et al. 1998). The way in which these authors have been able to so accurately separate digested food items is unclear but may be indicative of allocating loose, unidentifiable tissue to identifiable prey categories present in the gut. In this study 72.4% of stomachs contained only one identifiable prey type along with unidentifiable loose tissue (Table 2.1, Fig. 2.2). Allocating the loose tissue to the identifiable prey category in these stomachs would have resulted in occurrences of unidentifiable prey more similar to those listed in the references above. While it is probable that this approach would often correctly classify loose tissue, for example that the loose tissue in figure 2.2 is part of the easily identifiable digested fish, this cannot be visually confirmed and allocating it as such is not a rigorous, precise or accurate method of quantifying dietary composition.

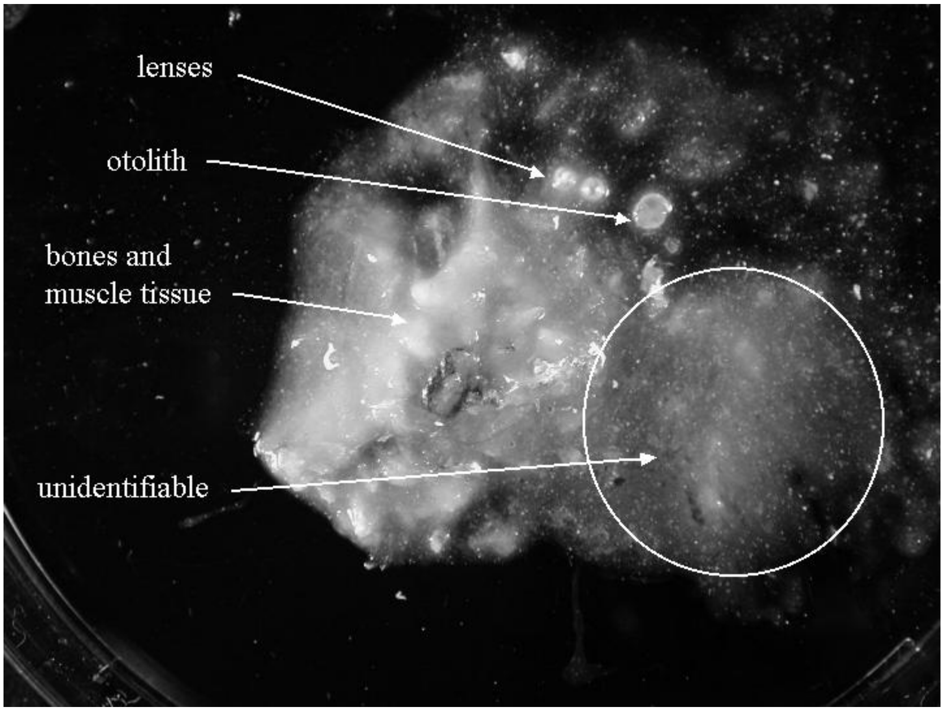


Figure 2.2: Partially digested fish remains from the stomach of a predatory fish. The accurate physical separation of unidentifiable tissue from identifiable fish tissue is not possible. While it seems probable that the unidentifiable tissue is part of the digested fish, this can not be visually confirmed and it may be a mixture of remains from prey types no longer represented by identifiable parts.

Because the identity of loose tissue cannot be confirmed visually, it can only be unambiguously classified as 'unidentified'. Furthermore, physically separating 'unidentified' loose tissue from partially digested remains is highly subjective; what is fish and what is loose tissue in figure 2.2? Consequently, quantifying the diets of the fishes examined in this study by volume or weight could only roughly approximate the dietary composition. Expressing percent contribution by volume or weight to one or two decimal places (see references above) would be unrealistic and provide a false sense of precision. When the additional confounding effects of sample size, differential digestion rates and order of ingestion are considered, data provided by the volumetric and gravimetric approaches are ambiguous and difficult to interpret (see below). In contrast, presence/absence data is precise and unambiguously interpretable because the values presented represent simply the proportion of individuals containing a particular positively identified prey type.

The criticisms expressed above may be less important, or not valid, in other systems or for other trophic groups. For example, species collected from cooler temperate waters, or those which primarily consume less fleshy prey such as planktonic crustaceans, may present less difficulty in accurately separating prey types. In such cases, volumetric or gravimetric quantification of gut contents could provide useful additional information on the relative amounts of each prey type consumed.

Hynes (1950) hinted at the problems of false accuracy in several of the methods, but only specifically discussed the problem of counting the number of prey items. Hynes points out that enumerating prey is realistically only an estimate of prey numbers because of the breakage of items into pieces. The advantage of 'simpler' methods such as frequency of occurrence over enumeration is that they "*avoid the unwarranted impression of accuracy which results from the use of counts…which has led some authors into basing a great deal of mathematical analysis on data which would appear to be fundamentally uncertain*" (Hynes 1950). The criticism I make here of volume or weight indices is not about the widely debated theoretical value of the information provided (Hyslop 1980), rather it is about the level of accuracy implied from data that are in practice "fundamentally uncertain", and the validity of detailed interpretation stemming from them.

2.2 Interpreting dietary composition. As well as being imprecise, inaccurate and time consuming to collect, it is difficult to interpret dietary data quantified by volume or weight. Sample size, differential digestion rate and the order of ingestion of different prey items interact to confound interpretations of dietary composition (Hyslop 1980, Haywood 1995). Additionally, unusual prey items in the gut of a single predator have the potential to greatly influence the data obtained by the 'bulk' measures. For example, Salini et al. (1990) report that 37 % of 214 *Arius proximus* contained fish prey, and that fish contributed 61.1 % of the total dry weight of prey consumed by this species. While it is easy to interpret the meaning of 37 % occurrence, i.e. that 79 of the 214 individuals had consumed fish, the meaning of 61.1 % dry weight of fish is ambiguous. In fact, one individual *A. proximus* had consumed a single large fish prey which accounted for 47 % of the total dry weight of prey consumed by the 214 individuals (Salini et al. 1990). Examples of such issues that confound interpretation of diets quantified by bulk are rarely reported or discussed, but likely to be quite common.

At small sample sizes the results obtained by bulk (volume/weight) can diverge considerably from those provided by frequency of occurrence (e.g. Salini et al. 1990, Haywood et al. 1998, Cortes 2001). This is because of the increased influence of unusual prey items, digestion rate and order of ingestion at small sample sizes. For example, a small sample of fish collected from one location at one time may have equal occurrence of two prey types, but a much greater contribution by bulk of one prey because either a) a greater bulk of that prey was consumed, b) that prey was consumed more recently, or c) has been digested more slowly than the other. Summaries of dietary composition by bulk make no distinction between these scenarios, even though their meanings are quite different, and thus interpretations of prey importance based on measures of bulk are ambiguous. This is exacerbated by the potential for a number of fish in one sample to have fed on a series of prey types in the same order, leading to a great overemphasis of the importance of the prey type consumed last or digested slowest. Consequently, at small sample sizes, dietary composition quantified by bulk can only be accurately interpreted and generalised as presence/absence anyway. These confounding factors have less influence on interpretations of frequency of occurrence data.

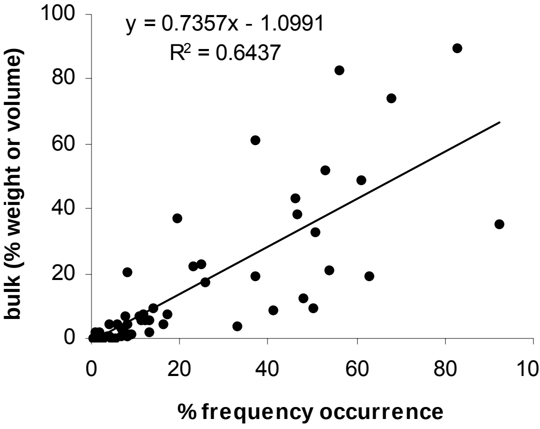


Figure 2.3: Contribution of prey items measured by both % frequency of occurrence and by bulk (either % volume or weight). Includes only data on mobile macroivertebrate and fish prey, for species with a sample size ≥ 100. Data from Salini et al. 1990, 1998, Schafer et al. 2002, Brancini & Perez 2005, and Xue et al. 2005.

In larger samples, with broad spatio-temporal distribution, the effects of digestion rate and order of ingestion are less influential on dietary compositions quantified by bulk because it is unlikely that there would be any consistent order of ingestion of particular prey types through space and time. In such samples, quantifying the diet by either bulk or by frequency of occurrence provides similar representations of the dietary composition (Fig. 2.3), thus making the more complicated methods redundant (Hynes 1950, MacDonald & Green 1983).

Even though the bulk indices provide similar information to frequency of occurrence at larger sample sizes, they are still imprecise and difficult to interpret relative to frequency of occurrence data. Additionally, because frequency of occurrence data are obtained directly from visual observation of the gut content, data on individual predators diets can be easily recorded, allowing for detailed examination of spatial, temporal and ontogenetic patterns in dietary habits. Therefore, to obtain robust, precise, accurate and unambiguously interpretable quantification of dietary composition of the predatory fishes examined in this study, the frequency of occurrence technique was the most useful approach.

Chapter 3

Redefining the piscivore assemblage of shallow estuarine nursery habitats

ABSTRACT

It is often suggested that there are few piscivorous fishes in shallow estuarine habitats worldwide, and consequently that these habitats are valuable as nurseries for juvenile fishes because they provide refuge from predation. Information on the dietary habits of predatory fishes from tropical estuaries remains limited to broad summaries that lack quantitative detail on the fish components of the diet. Consequently, it remains unclear which predators in shallow tropical estuarine nurseries target new recruits. To define the assemblage of piscivorous fishes relevant to the functioning of shallow water nurseries, the diets of predatory fishes collected over 6 years from shallow (<1.5m) sandy habitats in the lower reaches of 17 tropical estuaries were examined. Fifty-one taxa from twenty-one families fed on fish, and the piscivore assemblage included many taxa and size classes that have been previously overlooked. Piscivores ranged in size from 15 mm to 755 mm and the majority of taxa were piscivorous to some degree from sizes well below 100 mm. All of the smaller piscivores (<100 mm) preyed mainly on small new recruits while only some of the larger piscivores did so. The taxonomic and functional diversity in the piscivore assemblage, and the fish community as a whole, highlights the complexity of the role of predation in the functioning of shallow tropical estuarine

nurseries. Despite this complexity, it is apparent that predation has the potential to be a major structuring force on shallow water tropical estuarine fish communities.

3.1 INTRODUCTION

It is widely considered that estuaries in general and shallow estuarine habitats in particular are valuable nurseries because they provide abundant food and refuge from predation for small and juvenile fishes (eg. Blaber & Blaber 1980, McIvor & Odum 1988, Ruiz et al. 1993, Laegdsgaard & Johnson 1995). The refuge theory is based, in part, on reports of low abundances of piscivorous fishes within estuarine habitats (eg. Shenker & Dean 1979, Rozas & Hackney 1983, Boesch & Turner 1984, Patterson & Whitfield 2000). Sheaves (2001) reviewed the proposition of few piscivorous fishes in shallow estuarine habitats and concluded that it was ill-defined and lacking in evidence. Both ideas of refuge and of few predators must logically be placed in context relative to some alternate habitat(s). While several authors have compared abundances of fishes between potential nursery habitats (eg. Blaber 1980, Robertson & Duke 1987), the logistical difficulties of sampling fish from multiple habitats with comparable gears makes comparisons of abundances between habitats difficult (Sheaves 2001). It is, however, important to understand the process of piscivory within estuarine habitats, and its influence on their roles as nurseries (Blaber 1986) because such knowledge will ultimately lead to an understanding of how estuarine nurseries function and exactly what makes them valuable.

The level of predator-induced mortality of juvenile fishes is obviously the ultimate factor that determines the importance of predation within shallow water estuarine nursery grounds (Sheaves 2001). Because much of the shallow nursery habitat in tidal estuaries is intertidal, juvenile fishes utilising shallow waters cannot be site-attached and must use multiple habitats on a daily basis (Sheaves 2005). As a consequence, directly estimating mortality by monitoring changes in abundance is virtually impossible, and alternate approaches are needed to examine the role of piscivory. Detailed examination of diets of predators that prey on small juvenile fish is one useful approach to understand the role of predation in structuring shallow estuarine nursery fish assemblages.

While there is some detailed work on predator-prey dynamics in extensively studied temperate estuarine systems (eg. Juanes & Conover 1995, Buckel & Conover 1997, Juanes et al. 2001), there is far less information available for tropical estuaries in the Indo-West Pacific region. Predator-prey dynamics are likely to be different in topical systems because they contain very diverse fish assemblages with the number of species usually an order of magnitude greater than in temperate estuaries, sometimes exceeding 200 species (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, $19^0$21'S, $146^0$57'E) recorded year-round recruitment with a broad peak during the summer wet season between November and April (Robertson & Duke 1990b). Most species showed extended recruitment seasons (≥5 months) with irregular pulses of recruits appearing in the estuary during the 13 month study.

Dietary data on piscivorous fishes from the tropical Indo-West Pacific remains limited to broad summaries of the contribution of various prey types (Salini et al. 1990, 1998, Haywood 1998). There are no quantitative data available on spatial, temporal or predator-size related trends in piscivore diets, nor on the composition and size structure of fish prey within predator diets. As a consequence of this paucity of data, our understanding of predator-prey dynamics and the role of piscivory in the functioning of tropical estuarine nurseries is in its infancy.

Information on the diets of piscivorous fishes within estuaries is mostly limited to large piscivores (>100 mm) only (eg. Blaber 1980, Blaber 1986, Salini et al.1990, Patterson & Whitfield 1996, 2000). Some species-specific studies in North America (eg. Hartman & Brandt 1995, Buckel & Conover 1997, Buckel et al. 1999) and southern Africa (Blaber 1982, Martin & Blaber 1983), show a substantial impact of several species of small piscivores on estuarine fish assemblages. For example, predation by young of the year bluefish (*Pomatomus saltatrix*) had a significant impact on recruitment strength of juvenile striped bass (*Morone saxatilis*) in the Hudson River estuary (Buckel et al. 1999). Despite such evidence the assemblage of small potentially piscivorous fishes has been largely overlooked, particularly in the tropics.

There appears to be two reasons why small potential piscivores have been overlooked. Firstly, there is a common assumption that large piscivorous fishes will inflict greater mortality on prey fish populations than smaller piscivores because they are capable of consuming greater numbers of small juvenile fishes. However there is a lack of dietary data supporting this proposition (e.g. Blaber 1980). Secondly, prey fish have generally been poorly defined resulting in an equally vague definition of the relevant piscivore assemblage. Prey are rarely defined beyond ‘small’ or ‘juvenile’ fishes (eg. Blaber 1980, Patterson & Whitfield 2000) and with few exceptions (Scharf et al. 1997, Manderson et al. 1999, 2000) data on prey fish sizes are not presented. Considering that many ‘small’ prey fish may be adults of resident species such as gobiids (eg. Blaber 1986) and that in tropical estuaries juvenile fishes range from 10 mm new recruits (Robertson & Duke 1990b) to >500 mm lutjanids and serranids (Sheaves 1995), a clearer definition than simply ‘small’ or ‘juvenile’ is required. It is logical to examine predation on new recruits because these experience the highest levels of natural mortality (Sogard 1997), and small changes in early mortality rates can profoundly influence ultimate cohort strength (Yanez-Arancibia et al. 1994). Consequently, predation on new recruits has the potential to be a major structuring force on estuarine nursery fish assemblages, as it is in other systems such as coral reefs (e.g. Hixon & Carr 1997, Webster 2002, Webster & Almany 2002).

Any examination of the piscivore assemblage important in structuring shallow estuarine nursery assemblages must include consideration of the full range of potential predators, along with detailed descriptions of the composition of the fish component of their diets. There is currently a paucity of data relating to these two components, particularly for shallow tropical estuarine habitats. The aim of this chapter was to gain an understanding of the range of piscivorous fishes that prey on newly recruited fish in shallow (<1.5 m) tropical estuarine nursery habitats. Two specific questions were addressed: (1) which predatory fish present in shallow estuarine nurseries prey on other fishes, (2) what is the composition of the fish component of piscivore diets in terms of prey size and taxonomic identity. Once the predator assemblage has been identified, future research can examine the role of predation in structuring fish assemblages in tropical estuarine nurseries.

3.2 METHODS

3.2.1 Study sites and sampling. Fish were collected from 17 estuaries along a 250 km section of the coast of north Queensland, Australia (Fig. 3.1). Freshwater input to these estuaries is highly seasonal, with the climate dominated by distinct summer-wet and

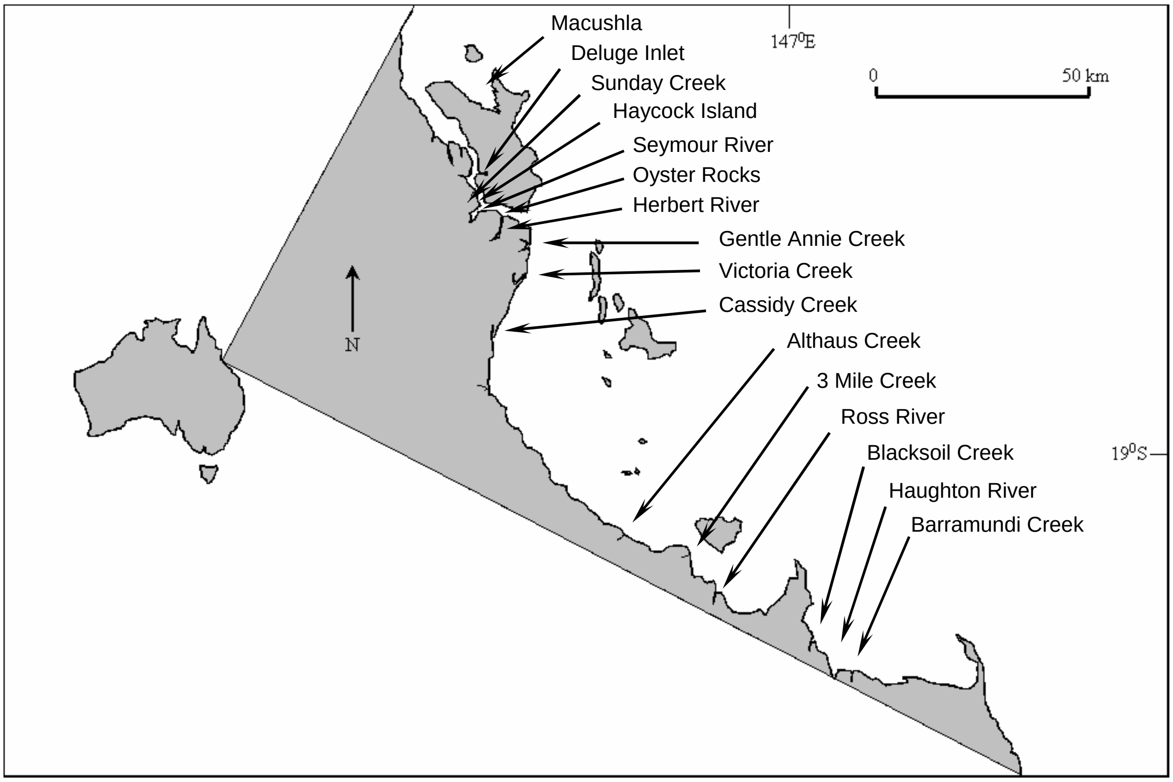


Figure 3.1: Estuarine sampling sites along the coast of north-eastern Queensland, Australia.

winter-dry seasons. Maximum tidal range is ca. 4 meters and extensive mixed mangrove forests are a feature of intertidal areas of estuaries throughout the region.

Sampling was conducted from July 1999 to January 2004. Sampling during recruitment periods would obviously be the most direct approach to determine which species prey on new recruits. However, as noted earlier, there are very few data on timing of recruitment of fishes into tropical estuaries in the Indo-West Pacific. What are available indicates year-round recruitment, with individual species appearing at irregular and unpredictable times during extended recruitment seasons (Robertson & Duke 1990b). Consequently, sampling effort was allocated as broadly as possible within the spatial and temporal limits of the study. Collections were made from the 17 estuaries on a total of 198 occasions covering 35 of the 55 months during the study, including samples representing every month of the year, providing a broad-scale temporal and spatial profile of piscivore diets. Representative samples of fish were collected from shallow (<1.5 m) sandy habitats in the lower reaches (≤5 km) of each estuary using a combination of 6 mm, 12 mm and 25 mm mesh seine nets. Additional samples were collected from the same locations with beam trawls, gill nets, cast nets and angling with artificial lures, to ensure that broad ranges of sizes of predators were represented. Sampling was concentrated on the lower reaches of the estuaries because these were the first shallow habitats available to new recruits entering the estuary. Although no published data are available on spatial patterns of fish recruitment within tropical estuarine systems, our observations indicate that most fish recruit to shallow waters in the lower reaches before dispersal throughout the system.

3.2.2 General Diets. Not all taxa sampled were included in gut content analysis, taxa occurring only rarely in our samples, or those with known non-piscivorous diets (e.g. Mugilidae) were excluded. Fish for dietary analysis were chilled in an ice bath immediately upon capture to halt the decomposition of gut content, and frozen as soon as possible afterwards. In the laboratory predators were identified, measured (fork length [FL] in mm), weighed (wet weight in grams) and their guts removed. Prey items were sorted and identified to as low a taxonomic level as possible. The presence of each prey type was recorded and the diets summarised as the frequency of occurrence of each prey type, that is, the percentage of total individuals within a size class or taxon that contained a particular prey (Hynes 1950, Hyslop 1980). Individuals with empty guts were not included in frequency of occurrence calculations. The prey category 'shrimp' includes unidentifiable shrimp-like crustacea, as well as alpheids, palaemonids and mysids. 'Other crustacea' includes a small number of crustaceans not defined in alternate categories, as well as highly digested crustacea, and as such may also include prey from the defined crustacean categories. The category 'other' includes a small number of prey types not defined in alternate categories. Unidentifiable tissue was only recorded (as 'other') when it was the only food present in the gut.

3.2.3 Major and minor piscivores. Initially, fish were categorised as 'major' or 'minor' piscivores using least squares univariate Classification and Regression Tree (CART) analysis based on the occurrence of fish in the diets (De'ath & Fabricius 2000). Previous authors have categorised predators as major piscivores if fish occur in more than

50 % of individuals (Whitfield & Blaber 1978), however univariate CART analysis provides a more objective method for categorising members of the piscivore assemblage. The technique successively splits the data into increasingly homogenous groups, by minimising the residual sums of squares for each split, analogous to least squares regression (De'ath & Fabricius 2000). In the current analysis, the residuals equal the difference between the overall average occurrence of fish across all taxa within a group and the occurrence of fish in the diet of each individual taxon. The 'best' tree model was chosen by bootstrapped V-fold cross validation using the Min. + 1SE rule (Breiman et al. 1984). Major piscivores identified by tree analysis and with samples sizes >35 were included in further analysis.

3.2.4 Trends and similarities in piscivore diets. Individual fish from each taxon were grouped into broad size classes using a series of non-metric multidimensional scaling (nMDS) analyses (one for each taxon) based on diet. For each taxon, fish were initially grouped into 5 mm size classes. Where necessary adjacent size classes were pooled to provide sufficient sample sizes per size class for analysis, while maintaining as much size resolution as possible. Apparent broad size classes identified by the individual species nMDS solutions were confirmed via hierarchical cluster analysis based on the same Bray-Curtis distance matrices used for each nMDS analysis. If analyses failed to identify discrete groupings because of some continuous trend in the diet across the size classes, equal size class groupings were made.

Once species had been split into broad size classes, all species were combined into a single data set. Similarities and trends in the diets of the abundant major piscivores were examined using (nMDS), based on Bray-Curtis dissimilarities calculated from the frequency of occurrence of each prey category in each size group of each taxon. Where the multi-species nMDS identified groups of taxa with similar diets, ontogenetic dietary models are only presented for a representative taxon from each group, rather than presenting multiple figures describing similar diets. Dietary models that detail ontogenetic trends in the diets of the major piscivores were produced using the lowess smoothing function (Cleveland 1979) on the frequency of occurrence of each prey type across the original fine size classes used in the individual species nMDS.

3.2.5 Prey fish size and identity. Where possible, fish prey were identified and measured (FL mm). In the case of highly digested fish prey, fish were identified to the lowest taxon possible from otoliths in the guts using a catalogue of photographs of the sagittal otoliths of common coastal and estuarine fishes from the region (Appendix A). The sizes of digested prey fishes were estimated using otolith weight-fish length relationships calculated from prey fishes collected from the same estuaries. Where prey fishes were only identifiable to genus or family, regressions combining all data for that genus or family were used to estimate prey size. R^2 values ranged from 0.84 to 0.99 for species-level regressions, and from 0.90 to 0.98 for genera and families (Appendix A).

Prey fish otoliths exposed to acidic digestive fluids in the stomachs of piscivores will gradually erode and thus those exposed for long periods (>2 hours) may be unreliable for estimating prey size (Jobling & Breiby 1986). Consequently the following precautions and validations were undertaken; (1) otoliths showing obvious signs of digestion such as loss of fine structural details were not used to estimate prey length, (2) comparison of length estimates and measurements from 27 fish prey in advanced stages of digestion and not morphologically identifiable, yet sufficiently intact to obtain length measurements, and with otoliths still encased within the otic capsule, revealed a high degree of accuracy in the length estimates from these prey (estimated length = 1.02*measured length, R^2=0.93), (3) there was little difference between the upper and lower boundaries of the predator-prey length relationships described by quantile regression (see below) for scatter plots including and excluding prey lengths estimated from otoliths free of the otic capsule but showing no signs of digestion. Thus, estimates of fish prey length from otoliths encased in the otic capsule, or exposed to but showing no signs of digestion were considered reliable, and were included in the predator-prey length relationships.

The boundaries of the predator-prey length relationships were described by least absolute values quantile regression (Scharf et al. 1998a). The boundaries were represented by the 90th and 10th quantiles as these provide consistent parameter estimates for sample sizes presented in this study (Scharf et al. 1998a). Quantile regression coefficient standard errors were estimated using 20 iterations of the bootstrap resampling technique described by Gould (1992).

3.3 RESULTS

3.3.1 General diets. A total of 69 fish taxa were sampled and examined for gut contents. Of these, 51 taxa from 21 families had fish in their diets (Table 3.1). The combined sample of the 51 taxa included 4985 individuals that contained food in the stomach. Nineteen of the fifty-one taxa had sample sizes of ten or less. The non-piscivorous taxa were dominated by *Leiognathus* spp. (Leiognathidae). Taxa that preyed heavily on fish were either exclusively piscivorous (Sphyraenidae and Scomberidae) or also consumed other mobile epibenthic/nektonic prey, mainly crustacea (eg. Carangidae, Platycephalidae) (Table 3.1). Only two individual *Sphyraena* juveniles and two *Scomberomorus semifasciatus* were recorded with anything other than fish in their guts, and each of these contained unidentifiable prey that was probably fish remains. Those taxa for which fish occurred only infrequently in the diet were primarily either planktivorous (eg. Ambassidae) or benthic invertebrate feeders (eg. Sillaginidae, Sparidae) (Table 3.1).

In 25 of the 51 taxa, the smallest individuals examined had consumed fish (Table 3.1a). Forty-two taxa had a minimum length of piscivory <100 mm, for 29 of these it was <50 mm. The smallest individual with fish in the stomach was a 15 mm FL *Pelates quadrilineatus.* Although nine taxa had a minimum length of piscivory >100 mm, the combined sample of these nine taxa included only one individual <100 mm (*Eleutheronema tetradactylum,* n = 5, n<100 mm = 1; Table 3.1b). Fish was the dominant prey in the diets of all nine taxa with minimum lengths of piscivory >100 mm (Table 3.1a).

Table 3.1: Summary of the diets of piscivorous fishes collected from shallow (<1.5m) sandy habitats in the lower reaches of 17 tropical estuaries, north Queensland, Australia. Diet is expressed as % frequency of occurrence of each prey type. N is the number of stomachs containing food. Min. FL pisc. is the minimum sized individual with fish present in the diet.
(a) Dietary summary of total sample, (b) summary of the occurrence of fish in the diets of individuals ≤100mmFL.

		(a)																		(b)	
Family	taxon	N	FL(mm) range	min. length pisc.	fish	gammarid	crab	Acetes	penaeid	shrimp	copepod	other crustacea	bivalve	gastropod	cephalopod	polychaete	insect	fish scales	other	n≤100mmFL	fish
AMBASSIDAE																					
	Ambassis interrupta	27	42-67	67	4	4	4	-	4	-	56	30	-	-	-	11	33	-	59	27	4
	A. nalua	38	17-82	49	26	-	-	-	-	5	11	16	-	-	-	-	-	-	61	38	26
	A. telkara	315	12-64	47	4	2	9	-	1	<1	53	22	<1	1	-	3	5	-	53	315	4
APOGONIDAE																					
	Apogonid sp. 1	1	61	61	100	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	100
BELONIDAE																					
	Belonidae juveniles	2	40-45	40	100	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	100
	Strongylura strongylura	34	77-350	77	62	-	-	6	12	-	-	6	-	-	-	-	-	-	26	4	75
	Tylosurus crocodilus	19	109-502	109	74	-	-	-	5	-	-	5	-	-	-	-	-	-	26	0	-
	T. gavialoides	15	122-365	122	93	-	7	-	-	-	-	-	-	-	-	-	-	-	7	0	-
CARANGIDAE																					
	Atule mate	10	214-274	214	100	-	-	-	-	-	-	10	-	-	-	-	-	-	-	0	-
	Caranx ignobilis	75	48-472	48	88	-	8	15	15	5	-	7	-	-	-	-	-	-	3	21	86
	C. sexfasciatus	45	28-265	28	78	-	2	2	13	9	-	11	-	-	2	-	-	-	16	37	76
	Gnathanodon speciosus	8	62-490	62	75	-	38	-	13	13	-	13	63	-	-	13	-	-	-	1	100
	Megalaspis cordyla	1	472	472	100	-	-	-	-	-	-	-	-	-	100	-	-	-	-	0	-
	Scomberoides commersonianus	39	25-755	26	54	-	-	8	28	5	-	-	-	-	-	-	-	13	10	20	25
	S. lysan	316	18-288	21	50	-	<1	1	10	7	2	21	-	-	-	<1	20	3	23	269	44
	S. tala	22	227-445	227	95	-	-	-	9	-	-	-	-	-	-	-	-	-	5	0	-
	Trachinotus botla	3	230-268	230	67	-	67	-	-	33	-	33	-	-	-	-	33	-	33	0	-
CENTROPOMIDAE																					
	Lates calcarifer	6	337-405	367	67	-	-	-	17	-	-	-	-	-	-	-	-	-	17	0	-
ENGRAULIDAE																					
	Stolephorus spp.	5	41-59	42	40	-	-	-	-	-	20	40	-	-	-	-	-	-	-	5	40
	Thryssa hamiltonii	9	66-207	83	22	-	-	11	33	-	-	22	-	-	-	-	-	-	22	8	25
GERREIDAE																					
	Gerres filamentosus	398	18-165	21	<1	8	-	-	2	-	49	6	12	5	-	13	-	-	75	393	<1
GOBIIDAE																					
	Butis butis	3	60-90	72	33	-	33	-	33	33	-	33	-	-	-	-	-	-	-	3	33
	Psammogobius biocellatus	130	22-84	27	62	20	2	2	5	5	2	10	<1	-	-	<1	-	-	9	130	62
LEIOGNATHIDAE																					
	Gazza minuta	12	34-74	63	25	-	-	-	-	-	-	8	-	-	-	-	-	-	67	12	25
LEPTOBRAMIDAE																					
	Leptobrama muelleri	10	190-267	190	100	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-
LUTJANIDAE																					
	Lutjanus fulviflamma	3	41-85	85	33	-	33	-	-	67	-	-	-	-	-	-	-	-	-	3	33
	L. russellii	16	20-48	20	44	6	-	-	-	19	6	44	-	-	-	6	-	-	13	16	44
	Lutjanus juveniles	3	23-41	41	33	-	-	-	-	33	33	33	-	-	-	-	-	-	-	3	33
PARALICHTHYIDAE																					
	Pseudorhombus arsius	321	16-276	20	65	22	14	2	15	7	-	15	-	<1	-	-	-	-	5	273	63
PLATYCEPHALIDAE																					
	Platycephalus arenarius	131	15-131	21	43	37	3	-	5	14	2	24	-	-	-	-	-	-	3	128	42
	P. endrachtensis	30	38-413	38	63	-	33	-	7	10	-	17	-	-	-	-	-	-	-	9	78
	P. fuscus	503	17-630	20	42	38	7	3	6	2	-	14	<1	-	-	<1	<1	-	10	386	32
	Suggrundus sp.	16	26-120	39	31	6	19	-	19	6	-	38	-	-	-	-	-	-	13	14	29
POLYNEMIDAE																					
	Eleutheronema tetradactylum	5	67-455	385	60	-	-	-	20	-	-	20	-	-	-	-	-	-	20	1	0
SCOMBERIDAE																					
	Scomberomorus semifasciatus	67	28-223	28	97	-	-	-	-	-	-	-	-	-	-	-	-	-	3	65	97
SILLAGINIDAE																					
	Sillago analis	187	22-217	58	2	34	5	-	3	6	31	28	5	2	-	9	12	-	43	162	2
	S. ciliata	151	32-206	57	9	22	9	-	3	9	34	30	13	1	-	9	11	-	48	106	8
	S. maculata	788	17-147	41	6	16	6	-	3	1	40	27	4	<1	-	32	1	1	46	766	6
	S. sihama	813	17-180	37	2	17	10	-	1	1	45	25	6	1	<1	13	1	<1	59	713	1
SPARIDAE																					
	Acanthopagrus australis	99	22-237	37	11	20	21	-	1	1	8	36	6	1	-	19	3	10	54	84	8
	A. berda	117	27-232	27	9	4	28	-	1	4	4	34	9	9	-	4	7	9	78	99	9
	Acanthopagrus juveniles	9	25-42	25	44	11	89	11	-	11	-	11	-	-	-	-	-	-	-	9	44
SPHYRAENIDAE																					
	Sphyraena barracuda	6	52-403	52	100	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	100
	S. jello	6	69-370	69	100	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	100
	S. obtusata	1	77	77	100	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	100
	Sphyraena juveniles	80	28-145	28	98	-	-	-	-	-	-	-	-	-	-	-	-	-	3	79	97
SYNODONTIDAE																					
	cf. *Saurida gracilis*	40	29-60	37	28	5	5	8	5	35	-	18	-	-	-	-	-	-	10	40	28
	Saurida sp. 2	14	37-87	37	93	-	-	-	14	7	-	7	-	-	-	-	-	-	-	14	93
TERAPONTIDAE																					
	Pelates quadrilineatus	5	15-56	15	20	-	40	-	20	-	20	20	-	-	40	-	-	20	-	5	20
	Terapon jarbua	13	35-86	35	46	-	8	-	23	-	-	23	-	-	-	15	-	69	23	13	46
URANOSCOPIDAE																					
	Ichthyscopus lebeck	18	15-91	22	67	-	-	-	-	-	-	56	-	-	-	-	-	-	-	18	67

3.3.2 Major and minor piscivores. There were two main groups within the piscivore assemblage based on the occurrence of fish in the diet (Fig 3.2). Minor piscivores comprised 3015 individuals in 15 taxa with a combined average occurrence of fish of 5 %. The remaining 1970 individuals in 36 taxa formed the major piscivores. These were further divided into three groups in the 'best' CART model, however most of the variability in the data set was explained by the first split, as shown by the relative lengths of the vertical branches of the tree (De'ath & Fabricius 2000). *Suggrundus* sp. had the

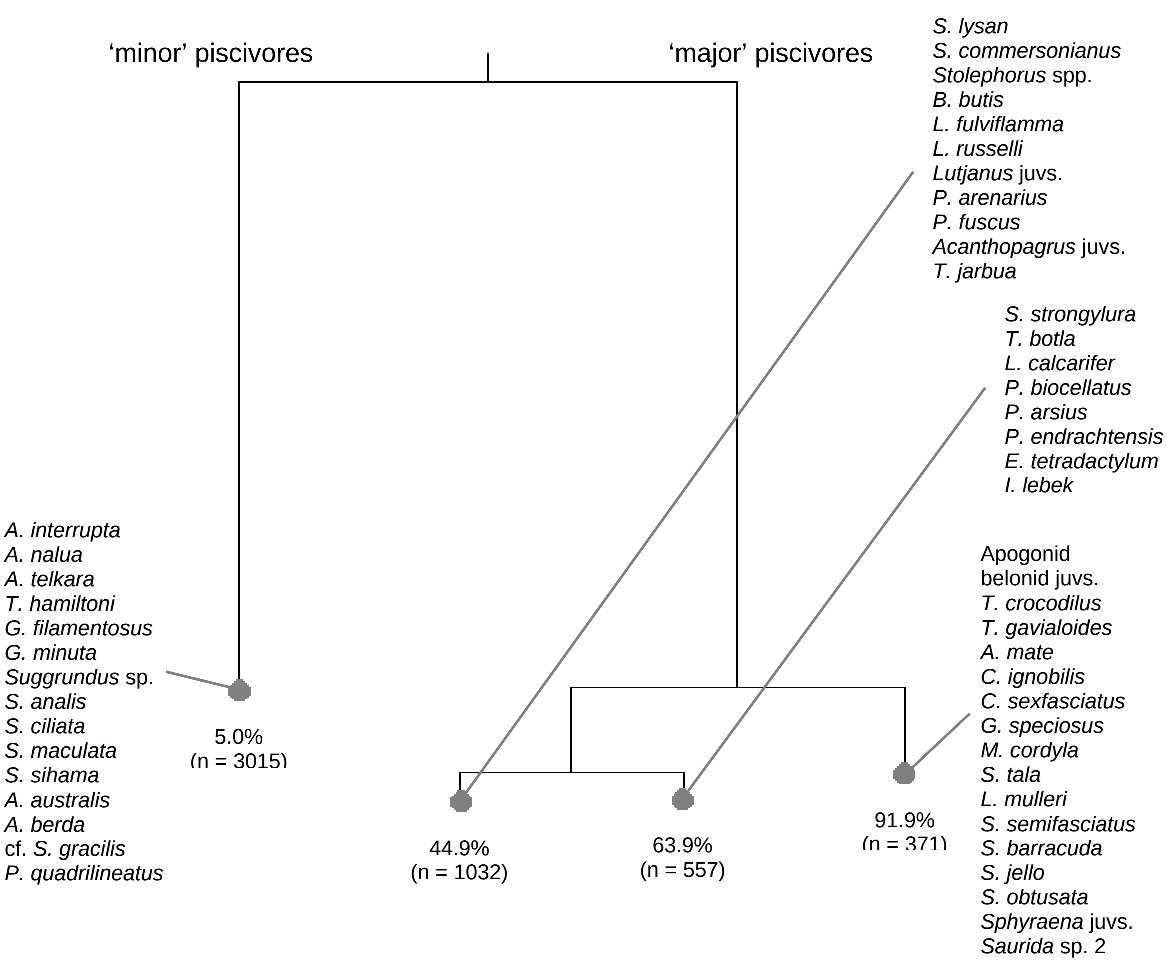
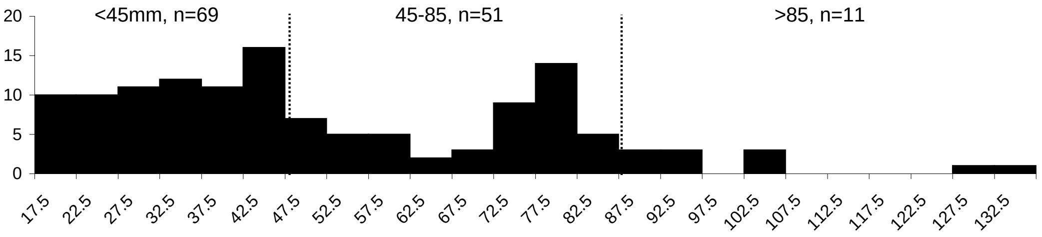


Figure 3.2: Four-leaf univariate Classification and Regression Tree defining major and minor piscivores based on the occurrence of fish in the diet. Sample sizes and average occurrence of fish within each group are shown below each leaf.

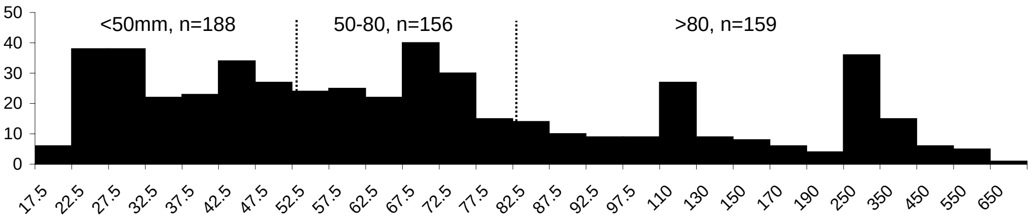
highest occurrence of fish of any of the minor piscivores, with 31 % of individuals containing fish, while *Butis butis,* with 33 %, had the lowest occurrence of fish prey among the major piscivores (Table 3.1a). Major piscivores with sample sizes >35 were included in further analysis. These were *Caranx ignobilis, C. sexfasciatus, Scomberoides commersonianus, S. lysan* (Carangidae)*, Psammogobius biocellatus* (Gobiidae)*, Pseudorhombus arsius* (Paralichthyidae)*, Platycephalus arenarius, P. fuscus* (Platycephalidae)*, Scomberomorus semifasciatus* (Scomberidae) and *Sphyraena* juveniles (Sphyraenidae). Three species of barracuda, *Sphyraena barracuda, S. jello* and *S. obtusata* were pooled with *Sphyraena* juveniles for further analysis because of the similarity in diets, the only identifiable prey in any *Sphyraena* spp. was fish (Table 3.1a).

Samples of the 10 abundant major piscivores included a broad range of sizes (Fig. 3.3). The fine size classes along the x-axis in figure 3.3 are those used in the individual species nMDS and in the smoothed ontogeny models. The dotted lines indicate the broad size classes used in the multi-species nMDS, as identified by the individual species nMDS and hierarchical cluster analysis. Neither *Sphyraena* spp. (Fig. 3.3i) nor *Scomberomorus semifasciatus* (Fig. 3.3j) showed any size related trends in dietary composition, with virtually all individuals consuming only fish (Table 3.1), thus the lack of broad size class divisions for the multi species nMDS analysis. The two individual *S. semifasciatus* >100 mm (Fig. 3.3j) were 213 mm and 223 mm FL.

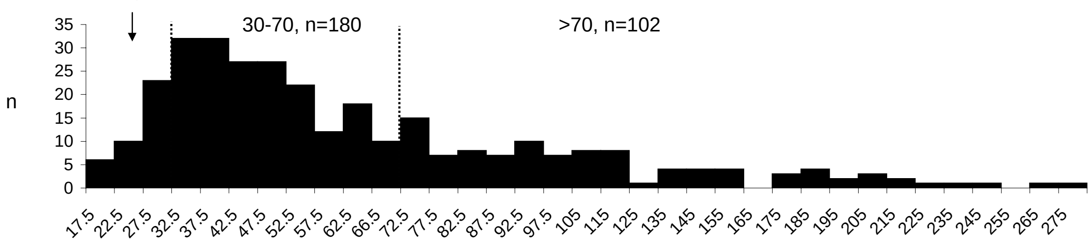
a) *Platycephalus arenarius*, n=131



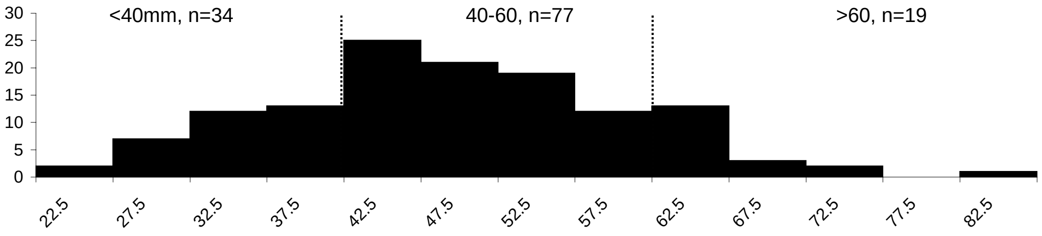
b) *P. fuscus*, n=503



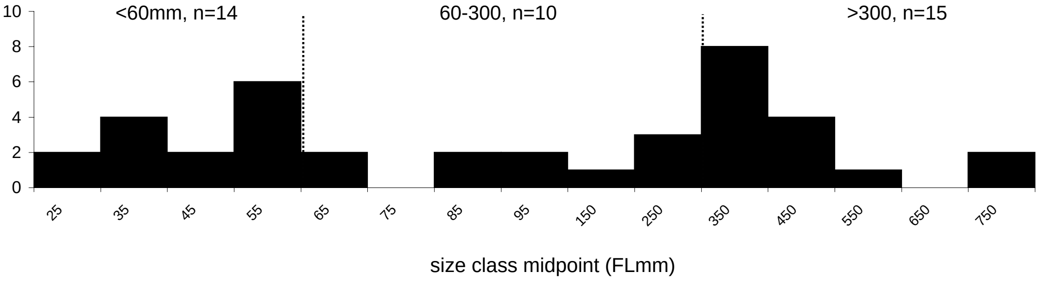
c) *Pseudorhombus arsius*, n=321



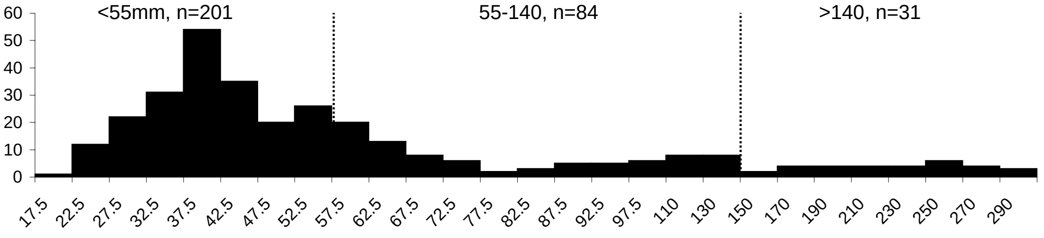
d) *Psammogobius biocellatus*, n=130



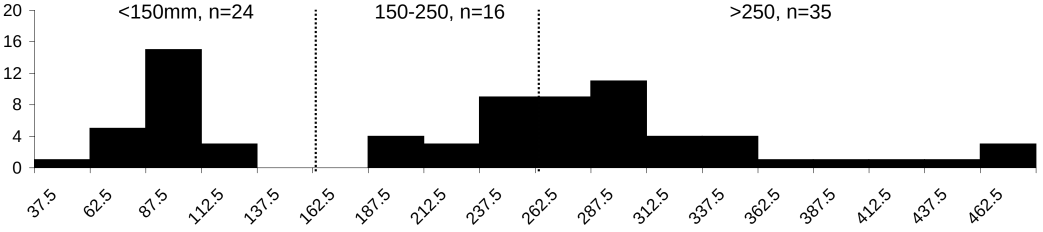
e) *Scomberoides commersonianus*, n=39.



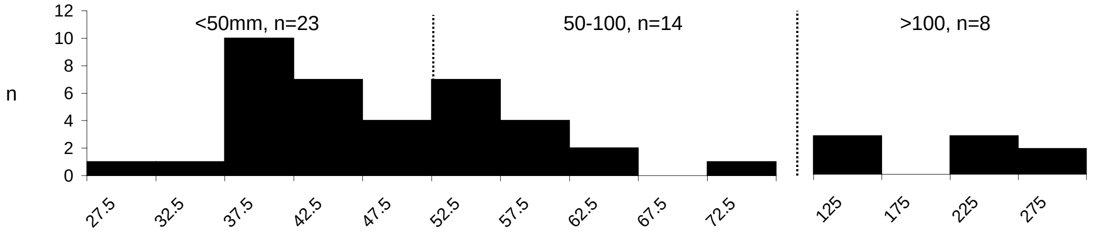
f) *S. lysan*, n=316



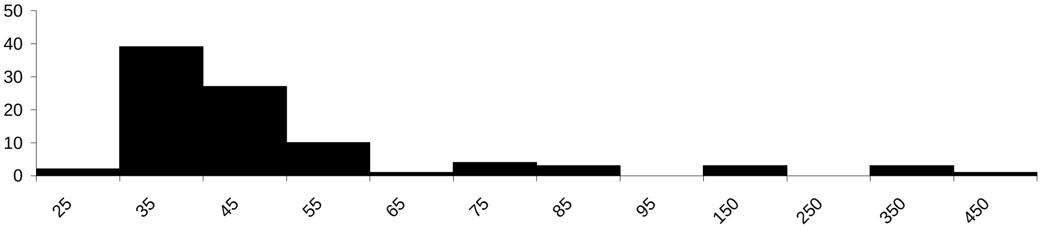
g) *Caranx ignobilis*, n=75



h) *C. sexfasciatus*, n=45



i) *Sphyraena* spp., n=93



j) *Scomberomorus semifasciatus*, n=67

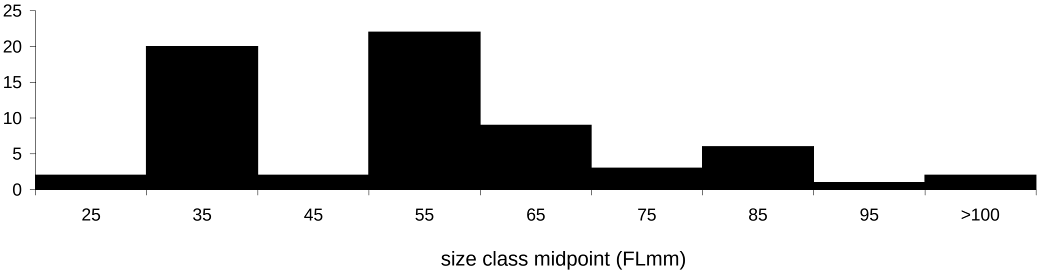


Figure 3.3: Size structure of samples of the abundant major piscivores used in further dietary analysis. Note that the size class widths are not constant in b), c), e), f), h), i) and j). For example, the size structure of the *Platycephalus fuscus* sample is presented in 5mm size classes from 15-100mm, 20mm size classes from 100-200mm and 100mm size classes from 200-700mm (Fig. 3b). Broad size classes used in the multispecies nMDS are indicated by dotted lines and sample size for each of these size classes is provided. For example, nMDS and cluster analysis on the diet of *Platycephalus fuscus* revealed 3 broad size classes: <50mm (n=188), 50-80mm (n=156) and >80mm (n=159) (Fig. 3b).

3.3.3 Trends and similarities in piscivore diets. Several of the abundant major piscivores showed ontogenetic shifts in relation to the contribution of fish in their diets, while others consumed fish at all sizes examined (Fig. 3.4a). *Platycephalus fuscus, P. arenarius* and *Pseudorhombus arsius* all had similar diets showing an ontogenetic shift from preying primarily on gammarid amphipods at small sizes to preying on fish at larger sizes (Fig. 3.4b group i, Fig. 3.5a). *Psammogobius biocellatus, Scomberoides commersonianus* and *S. lysan* showed a similar ontogenetic shift, preying mainly on fish at larger sizes, however small individuals of these taxa preyed mainly on penaeids and/or other crustacea (Fig 3.4b; group ii, Fig 3.5b). In contrast to *P. biocellatus* and *S. commersonianus,* insects were

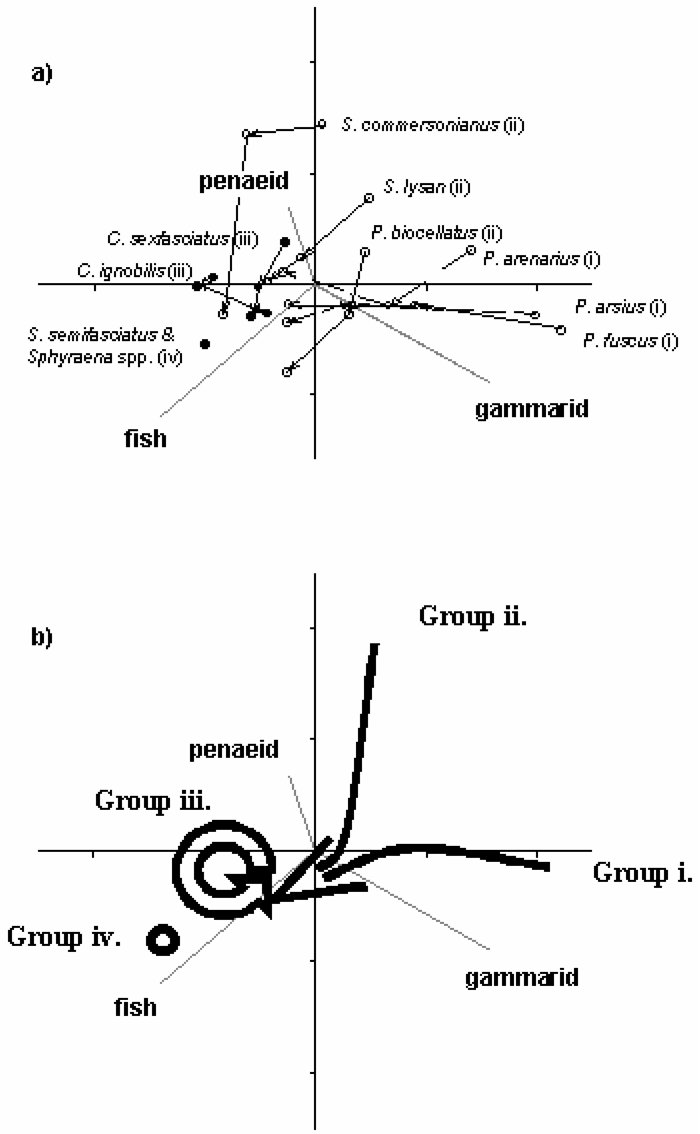


Figure 3.4: Dietary trends in the piscivore assemblage. (a) 2-dimensional non-metric multidimensional scaling solution using Bray-Curtis dissimilarities calculated from the frequency of occurrence of diet categories, stress = 0.11. Arrows link small to large broad size classes demarcated by dotted lines in figure 3.3. Vectors indicate the correlation of the original variables (prey categories) with the two dimensional space. Lengths of vectors are proportional to the partial R^2. Only prey categories with partial R^2 >0.35 are presented; fish 0.93, gammarid 0.91, penaeid 0.36. (b) simplified representation of groupings of major piscivores. Group identities are shown in parenthesis in figure 3.4a.

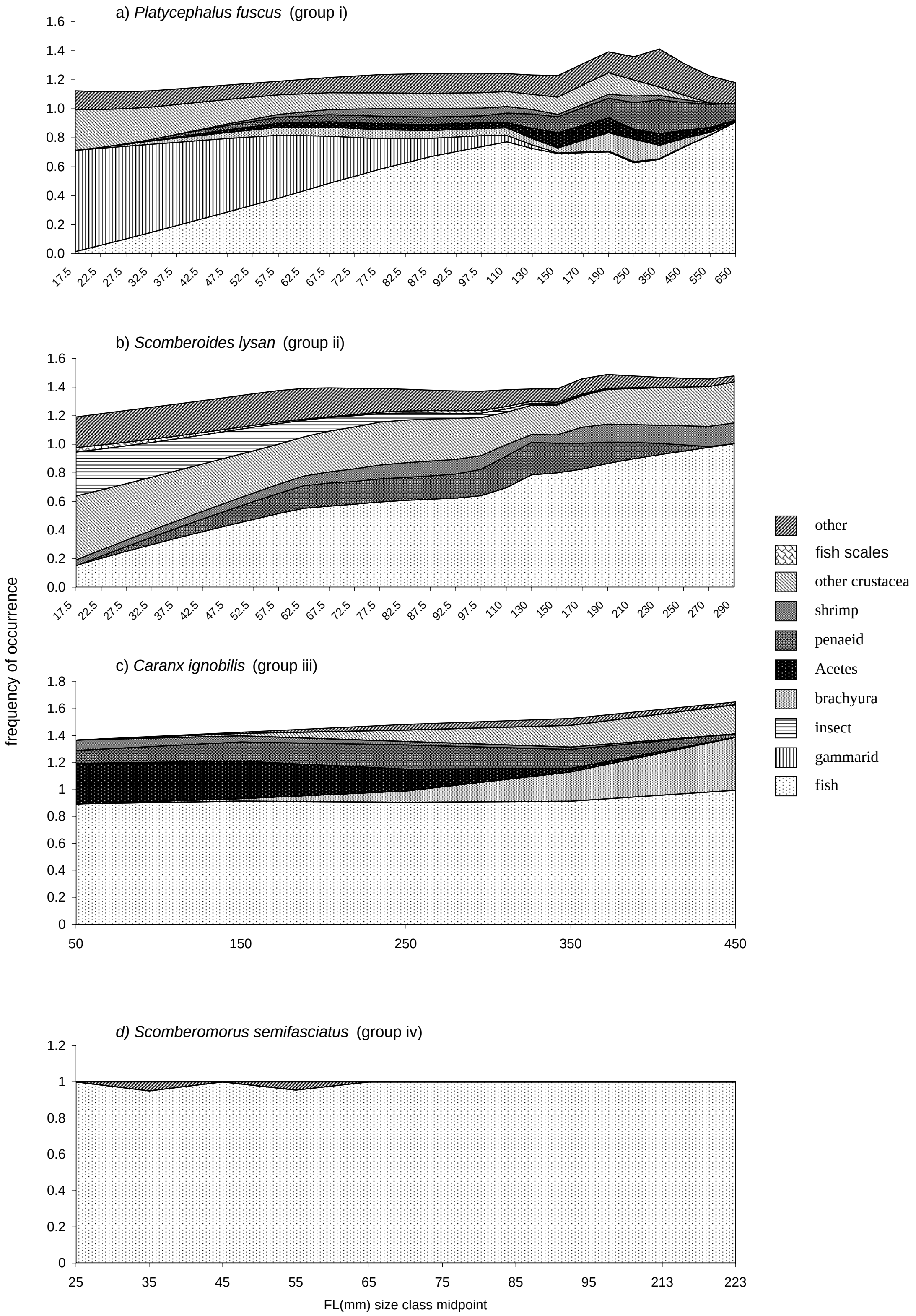


Figure 3.5: Representative ontogenetic dietary models for each of the four groups of major piscivores identified by nMDS (Fig. 3.4). Raw data were lowess smoothed with smoothing factors; a) 0.7, b) 0.7, c) 0.9, d) not smoothed.

a prominent part of the diet of small *S. lysan* (Fig 3.5b), otherwise their diets were similar (Fig 3.4a). Fish was dominant in the diet of *Caranx ignobilis* and *C. sexfasciatus* at all sizes examined, with smaller contributions of penaeids and other crustacea (Fig 3.4b; group iii, Fig 3.5c). *Scomberomorus semifasciatus* and *Sphyraena* spp. consumed fish almost exclusively (Fig 3.4b; group iv, Fig 3.5d).

3.3.4 Prey fish size and identity. The piscivore assemblage consumed a range of fish prey, with small juvenile *Leiognathus* spp., *Sillago* spp. and *Gerres filamentosus* common in the diets of most of the abundant major piscivores (Fig. 3.6). The gobid *Acentrogobius viridipunctatus* was another common small fish prey, present in the diets of all the abundant major piscivores except *Scomberoides commersonianus*. The four prey taxa listed above were common in the diets of most of the other piscivores examined (Table 3.1). Additionally, clupeoid fishes (including *Stolephorus* spp., *Herklotsichthys* spp., *Sardinella* spp. and unidentified clupeoids) were prominent in the diets of the carangids (eg. Fig. 3.6e-h). Many of the prey fish present in the smaller piscivores (<50 mm) were larvae or small new recruits that were unidentifiable due to a lack of distinguishing morphological features of the partially digested prey fish at these small sizes (eg. Fig. 3.6a).

Seven identifiable fish prey consumed by the three *Sphyraena* spp. >120 mm FL, and the one identifiable fish in the stomach of the 213 mm *Scomberomorus semifasciatus* were not included in quantile regressions (Table 3.2) or presented in the predator-prey size relationships (Fig. 3.6i,j). For *Sphyraena* spp. >120 mm, both the largest (155 mm

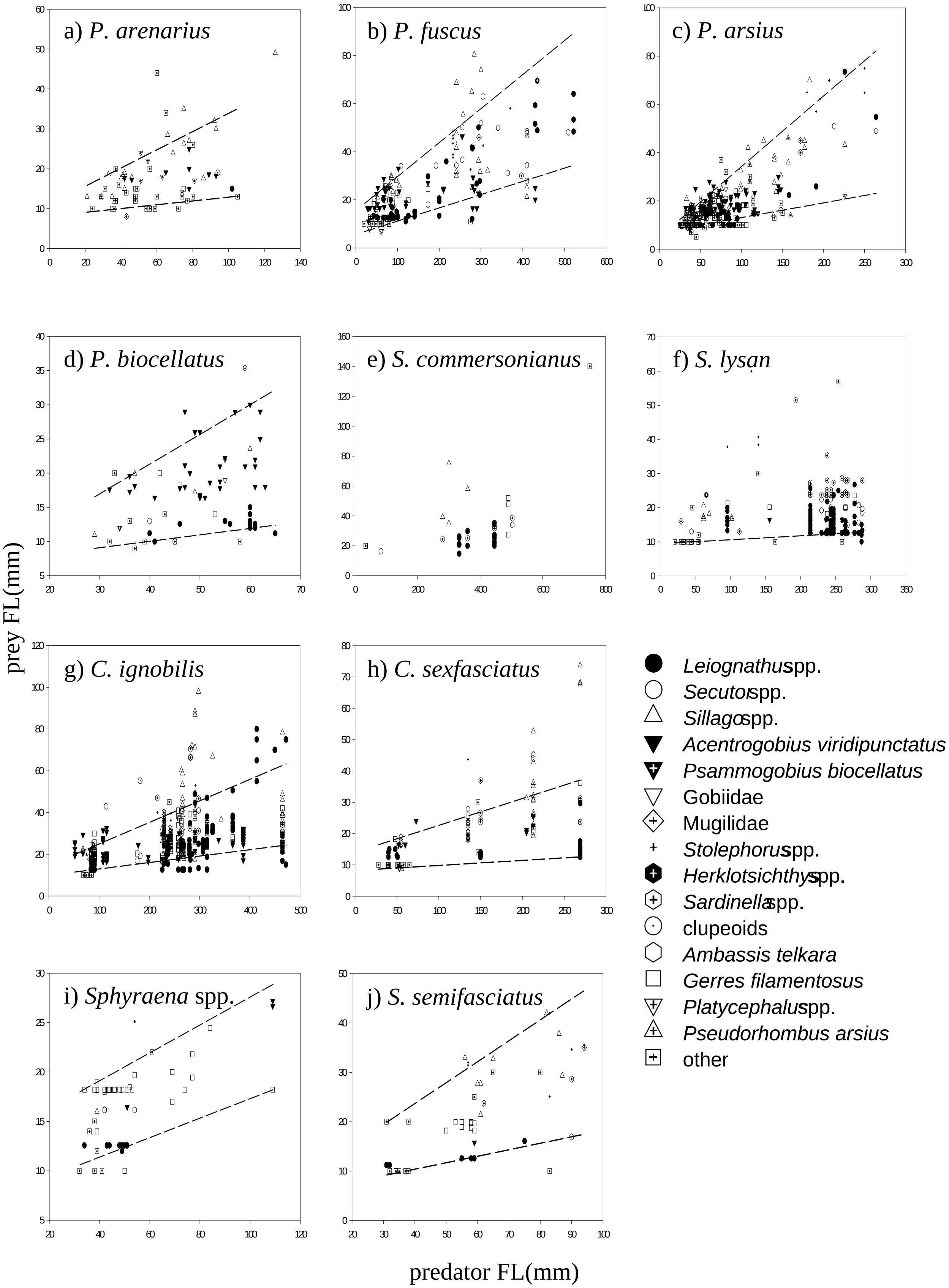


Figure 3.6: Size and taxonomic identity of fish prey in the diets of the abundant major piscivores

clupeid in a 370 mm *S. jello*) and smallest (32 mm *A. telkara* in 394 mm *S. barracuda*) of the seven prey were highly influential points in the quantile regressions such that 90th, 95th, 99th and the 10th, 5th, and 1st quantiles all passed through the upper and lower points respectively. Inclusion of the prey-size data for the three *Sphyraena* spp. >120 mm in the scatter plots compacted the bulk of the data, making the composition and boundaries of prey consumed by *Sphyraena* spp. <120 mm FL uninterpretable (Fig 3.6i). Similarly, the one identifiable fish in the stomachs of *S. semifasciatus* >100 mm, a 48 mm *Leiognathus* spp. in a 213 mm *S. semifasciatus*, was excluded from quantile regression and the scatter plot (Fig. 3.6j).

Table 3.2: Slope estimates (± SE) for the upper (90th quantile) and lower (10th quantile) boundaries of predator-prey length relationships of the abundant major piscivores, as determined by quantile regression. n = number of fish prey shown in Figure 6 and used in quantile regression.

		quantile	
Taxon	n	10th	90th
Platycephalus arenarius	72	0.057 ± 0.004***	0.227 ± 0.014***
P. fuscus	180	0.041 ± 0.002***	0.131 ± 0.003***
Pseudorhombus arsius	306	0.060 ± 0.003***	0.292 ± 0.006***
Psammogobius biocellatus	71	0.092 ± 0.007***	0.432 ± 0.024***
Scomberoides commersonianus	35	-	-
S. lysan	258	0.011 ± <0.001***	NS
Caranx ignobilis	536	0.031 ± 0.001***	0.104 ± 0.005***
C. sexfasciatus	176	0.016 ± <0.001***	0.085 ± 0.006***
Sphyraena spp.	62	0.097 ± 0.014***	0.140 ± 0.031***
Scomberomorus semifasciatus	48	0.122 ± 0.018***	0.422 ± 0.019***

notes: NS P>0.05; *P<0.05; **P<0.01; ***P<0.001; - insufficient data for analysis

The largest individual *Platycephalus fuscus, Pseudorhombus arsius*, *Scomberoides commersonianus, Sphyraena* spp. and *Scomberomorus semifasciatus* did not consume small new recruits, while the remaining major piscivores consumed small fish across the entire size range examined (Fig. 3.6, Table 3.2). Large *S. lysan, C. ignobilis* and *C. sexfasciatus* individuals consumed small fish prey, close to the smallest fish consumed by any individual of these species (Fig. 3.6f-h). The relatively constant minimum prey size is reflected by the low slope estimates for the lower boundaries (10th quantile) of the predator-prey size relationships, as estimated by quantile regression (Fig. 3.6f-h; Table 3.2). The trend for these species to consume relatively small fish prey is also shown by the low (*C. ignobilis, C. sexfasciatus*) or non-significant (*S. lysan*) slope estimates for the upper boundaries (90th quantile) of the predator-prey size relationships (Fig. 3.6f-h; Table 3.2). These species mainly consumed fish prey much smaller than the maximum size they are capable of ingesting, as indicated by the spread of data above the upper boundary (Fig. 3.6g,h). In contrast, the remaining piscivores regularly consumed fish prey close to the maximum size recorded (Fig. 3.6a-d, i, j). These piscivores showed an increase in both the maximum and minimum fish prey size consumed (Fig. 3.6a-d, i, j; Table 3.2) and the slopes of their lower boundaries were similar to the slopes of the upper boundaries of the carangids (Table 3.2). *Psammogobius biocellatus* and *Scomberomorus semifasciatus* consumed fish prey that were large relative to the predators body size (Table 3.2) including several prey that were greater than 50 % of the predators length (Fig. 3.6d,j). The sample size of fish from the diet of *S. commersonianus* was too small to analyse using quantile regression, however the expected positive relationship between predator and prey size is apparent (Fig. 3.6e). The dense vertical stacks in the predator-prey relationships for *Scomberoides lysan, Caranx ignobilis* and *C. sexfasciatus* indicate the consumption of large numbers of fish by individual predators (Fig. 3.6f-h).

Individuals of the other abundant major piscivores tended to consume fewer prey per predator (Fig. 3.6a-e, i, j).

3.4 DISCUSSION

The piscivore assemblage of the shallow estuarine habitats sampled in this study included a diverse range of taxa over a broad range of sizes. Individuals consuming fish ranged in size from a 15 mm *Pelates quadrilineatus* up to a 755 mm *Scomberoides commersonianus* (Table 3.1). Only 9 taxa had a minimum length of piscivory >100 mm. These taxa had small sample sizes (n≤22) and the combined sample included only one individual <100 mm. All nine were categorised as major piscivores with fish dominating their diets, so despite the small sample sizes it seems likely that smaller individuals of these taxa would be piscivorous to some degree. Based on average predator-prey length ratios reported in literature on piscivory, Sheaves (2001) demonstrated that new recruits of 15 – 25 mm would be vulnerable to predators between 38 – 64 mm. In the present study the majority of taxa contained individuals that were piscivorous at these or smaller sizes. Many piscivores were much smaller than those previously considered as potentially important predators in estuarine nurseries (eg. Salini et al. 1990, Paterson & Whitfield 2000). The piscivore assemblage included both small species (eg. *Psammogobius biocellatus*) and small juveniles of species for which larger individuals have been considered important piscivores elsewhere (eg. *Scomberoides commersonianus,* Salini et al. 1990). The proposition that shallow water habitats in tropical estuaries provide small juvenile fishes with refuge from predation because there are few large piscivorous fishes (eg. Blaber 1980), fails to recognise the importance of the many small piscivores present in these habitats.

3.4.1 Sampling design. As with many previous studies (eg. Salini et al. 1990, Haywood et al. 1998) the dietary data presented here are pooled over fish collected from many locations on many occasions. This has several implications in relation to the interpretation of the dietary models presented, and their overall relevance to the importance of piscivory in shallow estuarine nurseries. Data pooled across sampling times and locations provides no information on temporal and spatial patterns in dietary habits. Information on diet variability is important in understanding the influence of processes such as prey availability, prey selectivity and the co-occurrence of predators and prey, all of which contribute to complex predator-prey dynamics that structure fish assemblages (eg. Juanes & Conover 1995, Juanes et al. 2001). However, such processes cannot be examined without first having a clear understanding of the relevant assemblage of predators and prey. Given our lack of basic knowledge of the diverse fish faunas of tropical estuarine systems (Blaber 2000), the aim of this chapter was not to examine spatial and temporal patterns in predation dynamics, rather to identify the relevant piscivore assemblage as a baseline from which to examine these patterns in future. Consequently, the dietary data presented here should not be interpreted beyond being a general representation of the dietary habits of members of the shallow water tropical estuarine fish assemblage.

Early mortality rates can have a major influence on ultimate cohort strength (Yanez-Arancibia et al. 1994) and predation on small fish during and shortly after their recruitment to shallow estuarine nurseries may be significant in structuring estuarine fish assemblages. Predation on newly settled fish is a major structuring force on coral reef fish communities (eg. Carr & Hixon 1995, Hixon & Carr 1997, Webster & Almany 2002), and in extreme cases has the potential to cause recruitment failure (Webster 2002). This chapter identifies a range of piscivores that consume small fish using shallow estuarine nursery grounds. Because recruits appear in the nursery year-round, with patchy recruitment within broad seasons for individual taxa (Robertson & Duke 1990b), allocating sampling effort as widely as possible was a logical approach to gain insight into the range of potentially important piscivores in shallow tropical estuarine nurseries. Importantly, this sampling design would underestimate the level of impact of various piscivores on new recruits because the patchy nature of recruitment means that the data presented include samples of predators from times when new recruits were not available. What the design does allow is an overview of the piscivore assemblage that prey on new recruits, as well as providing insight on the range of strategies within the piscivore assemblage.

3.4.2 Major and minor piscivores. Nineteen of the piscivore taxa (2 minor & 17 major piscivores) had sample sizes of ten or less (Fig. 3.2, Table 3.1). Such small sample sizes may not adequately represent a species diet and consequently the classifications of taxa with small sample sizes as major or minor piscivores should be interpreted with caution.

It is possible that with larger samples of these taxa, some of the major piscivores would have been classified as minor piscivores and vice versa.

While the major piscivores described here and elsewhere are likely to be important predators simply because they consume fish most of the time, the minor piscivores may also play an important role in structuring shallow water nursery assemblages. Many of the minor piscivore taxa, such as the ambassids, engraulids and sillaginids, dominate the shallow water fish communities of tropical Indo-West Pacific estuaries (Blaber 1980, Blaber et al. 1985, 1989, Robertson & Duke 1987, 1990a). Martin and Blaber (1983) concluded that small *Ambassis* spp. in southern African estuaries were at least as significant a group of predators as the larger, primarily piscivorous fishes. This is because although fish were rarely dominant in the diet, periodic predation on fish eggs and fry during spawning and recruitment periods, combined with the high abundances of *Ambassis* spp. resulted in great potential of these mainly planktivorous fishes to impact fish recruitment strength (Martin & Blaber 1983).

When the abundance of various piscivores is considered it becomes clear that the relative contribution of fish to the diets does not necessarily reflect the relative importance of each piscivore. One of the species studied by Martin and Blaber (1983), *Ambassis gymnocephalus* (called *A. telkara* in this study (Komori 2001)), has been recorded as highly abundant in estuaries along the north coast of Australia (Blaber et al. 1985, 1989), and northeastern Queensland (Robertson & Duke 1987, 1990a, 1990b). For example, *A. telkara* constituted 29.3 % by numbers and dominated the biomass of the shallow water fish fauna from Alligator creek near Townsville, Australia (Robertson & Duke 1990a, b). Even if the average occurrence of fish in the diet (4 % in this study) represents the level of predation by these on juvenile fish recruiting to the nursery such that only 4 % of individual *A. telkara* were piscivorous during a recruitment event, piscivorous ambassids alone would outnumber the combined assemblage of major piscivores recorded by Robertson and Duke (1990a). Many of the juvenile fish utilising shallow nursery habitats in tropical estuaries are minor piscivores (eg. Salini et al. 1990, Haywood et al. 1998, this study), yet their potential impact on nursery fish assemblages has not previously been discussed. Given the probability that the average low occurrence of fish in the diets of many minor piscivores represents switching from alternate prey to briefly targeting new recruits during recruitment events (Martin & Blaber 1983), new recruits entering shallow tropical estuarine nurseries would encounter far more predatory 'minor' piscivores than large primarily piscivorous fish. The combined mortality inflicted by minor piscivores could be significant in structuring tropical estuarine nursery fish assemblages and is worthy of further investigation.

3.4.3 Trends and similarities in piscivore diets. There are several patterns of ontogenetic changes in the contribution of fish in the diet of piscivores examined in this study. Minor piscivores, by definition, have a low frequency of occurrence of fish in their diets, and no clear relationship between predator size and the occurrence of fish is apparent. The low occurrence of fish in the diets of minor piscivores represents either some constant low level of consumption of fish prey, or switching from alternate prey to target new recruits during recruitment events (see discussion of 'Major and minor piscivores'). Among the major piscivores, some taxa showed ontogenetic shifts from alternate prey to fish with increasing predator size, for others fish dominated the diets at all sizes examined (Fig. 3.4). *Caranx ignobilis* and *C. sexfasciatus* may undergo ontogenetic dietary shifts at sizes smaller than sampled in this study, however these were primarily piscivorous across all sizes sampled (Fig. 3.4, Fig. 3.5c).

The range of predation strategies coupled with extended spawning seasons and irregular recruitment pulses of both predator and prey (Robertson & Duke 1990b) result in a complex mosaic of co-occurrence of predators and prey, making it difficult to predict the exact assemblage of piscivores awaiting new recruits to the nursery. This highlights the challenge confronting researchers in diverse tropical estuarine systems to uncover detailed predator prey relationships such as those examined in temperate estuaries (eg. Juanes & Conover 1995, Buckel & Conover 1997, Buckel et al. 1999, Juanes et al. 2001).

3.4.4 Prey fish size and identity. The piscivore assemblage consumed a range of prey including many small fishes. Among the common prey fish taxa found in this study, *Ambassis telkara* and three species of *Leiognathus* first appeared in samples from a nearby estuary at between 10 and 20 mm in length, followed by rapid growth within the nursery (Robertson & Duke 1990b). Our observations indicate that most of the common prey fish taxa found in this study recruit to the nursery at around this size. Another common small fish prey, the gobiid *Acentrogobius viridipunctatus* is a small species occurring at sizes between 10 and 50 mm in shallow sandy estuarine habitats in this region (Sheaves unpubl. data). Despite its small size, it is likely that *A. viridipunctatus*

<20 mm are also relatively new recruits to the nursery. It is therefore reasonable to conclude that the majority of fish prey <20 mm consumed by predators in this study were new recruits.

All of the smaller (<100 mm) piscivores examined in this study preyed primarily on small new recruits (eg. Fig. 3.6). Large individuals of the carangids *Scomberoides lysan, Caranx ignobilis* and *C. sexfasciatus* consumed a broad size range of fish prey, including large numbers of small new recruits. In contrast, larger individual *Platycephalus fuscus* and *Pseudorhombus arsius* did not prey on new recruits <20 mm. Based on the slope of the lower boundary of the predator-prey size relationship for *Platycephalus arenarius,* and the sparse available data for larger *Sphyraena* spp. and *Scomberomorus semifasciatus,* it is probable that larger individuals of these species would mostly consume relatively large fish prey (Fig. 3.6; Table 3.2).

While some large piscivores do consume large numbers of small fish prey as suggested by Blaber (1980), this cannot be generalised to apply to the whole piscivore assemblage of shallow water nurseries. Large individuals of several common piscivores do not appear to prey heavily on small new recruits, while small individuals of all piscivorous species are physically constrained to consume small prey. Juveniles of many members of the piscivore assemblage such as the carangids, sphyraenids and scomberids are commonly reported from estuaries in the tropical Indo-West Pacific (Blaber 1980, Blaber et al. 1985, 1989, Blaber & Milton 1990). Consequently new recruits to the shallow nursery are going to encounter far more small piscivorous fishes than large ones.

3.4.5 Implications and conclusions. The shallow water nursery habitats examined in this study contained an assemblage of piscivores that was diverse in terms of species composition, size structure, predation strategies and prey types. The diversity in the estuarine fish communities and the unpredictable timing of recruitment of either predators or prey highlight the challenge in predicting predation pressure on new recruits entering shallow estuarine nurseries in this region. It is clear however that the piscivore assemblage is far larger and more diverse than previously considered (eg. Blaber 1980, Salini et al. 1990) and has potential to be a major structuring force on estuarine fish communities.

Within the piscivore assemblage it is difficult to determine relative impacts of different piscivores on prey fish populations. Individual carangids can consume large numbers of demersal juveniles utilising the shallow nursery (eg. *Leiognathus* spp., *Sillago* spp. and *Gerres filamentosus*) but also prey heavily on pelagic clupeoids (Fig. 3.6e-h). Mobile predators such as the carangids may only feed sporadically in shallow water habitats, in a similar manner to their transient feeding on coral reefs (Hixon & Carr 1997). The coexistence of pelagic and demersal prey adds further complexity to the structuring of predation pressure by carangids on individual cohorts of recruits in the shallow nursery. The more sedentary piscivores such as platycephalids, and the small and minor piscivores, tend to consume fewer fish prey per predator but feed mainly on demersal fish prey and probably spend most of their time within the shallow nursery. The combined impacts of the mobile and sedentary piscivores in shallow tropical estuarine nurseries may be analogous to the effects of transient and resident piscivores that combine to structure coral reef fish communities (Hixon & Carr 1997).

In addition to the range of predation strategies, the relative abundance of different members of the piscivore assemblage will contribute significantly to the overall impact of each species or size class of piscivore on prey fish populations. However, it is difficult to compare the abundances of piscivores with different susceptibilities to different gears, thus presenting a significant challenge in assessing their relative impacts on prey fish populations. Despite such challenges, it is apparent from the clearer definition of the piscivore assemblage provided by this study that there is great potential for significant mortality of fish recruiting into shallow tropical estuarine nurseries. The idea that shallow nursery habitats have low predation pressure because of few large primarily piscivorous fishes is clearly too simplistic a view of nursery ground functioning. While this chapter contributes little to our understanding of the impact of predation in shallow estuarine waters relative to alternate nursery habitats and thus to our understanding of estuarine nursery ground value, it shows clearly that predation may be a major structuring force shaping shallow water estuarine fish assemblages.

Chapter 4

Refugees or ravenous predators: detecting the impacts of predation in an inherently patchy environment

ABSTRACT

Shallow water estuarine habitats are considered to provide small juvenile fishes with refuge from predation due, in part, to the apparent low numbers of piscivorous fishes. However, around the world many of the most abundant small and juvenile fishes that utilise these habitats consume other fish to some degree. Because of the low average occurrence of fish in the diets of these 'minor' piscivores, they have rarely been considered as potentially important predators in estuarine systems. However, predation by abundant minor piscivores on new recruits when they first enter the nursery may create a significant bottleneck at this critical life-history stage. To determine the potential importance of minor piscivores as predators on new recruits, spatio-temporal patterns in the diets of minor piscivores were examined and related to patterns of recruitment in shallow (<1.5 m) sandy habitats in a tropical 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. However, examination of spatio-temporal variability in the consumption of fish prey by minor piscivores sampled over 6 years from 17 estuaries in the region revealed that the low average occurrence of fish in their diet was a poor reflection of the spatial and temporal patterns in predation pressure by these on fish prey. Most of the time, minor piscivores did not consume fish prey, occasionally a large proportion of them did so. At particular times within individual estuaries multiple species of

minor piscivores preyed heavily on fish prey. When minor piscivores consumed fish prey, they preyed mainly on small new recruits. Thus, the evidence suggests that many small and juvenile fishes believed to gain refuge in shallow estuarine nurseries may themselves be important predators on fish recruiting to these habitats, and if so, may play a significant role in structuring estuarine fish faunas.

4.1 INTRODUCTION

Shallow water estuarine habitats are widely considered as valuable nurseries because they are believed to provide small juvenile fishes with refuge from predation due, in part, to the apparent low numbers of piscivorous fishes (e.g. Blaber 1980, Blaber & Blaber 1980, McIvor & Odum 1988, Paterson & Whitfield 2000). However, typically only primarily piscivorous fishes have been considered as potentially important predators in these systems (e.g. Blaber 1980, Hartman & Brandt 1995, Buckel et al. 1999, Paterson & Whitfield 2000). Occasional or ‘minor’ piscivores, those predators that on average have a low occurrence of fish in their diets (Whitfield & Blaber 1978a), have largely been ignored (Sheaves 2001, Chapter 3), despite the fact that such fishes are often dominant members of shallow water estuarine assemblages around the globe (e.g. Europe, *Pomatoschistus* spp., Hampel & Cattrijsse 2004, Pasquaud et al. 2004; *Clupea harengus*, Maes et al. 2003; southern Africa, *Ambassis* spp., Martin & Blaber 1983; North America, *Morone americana*, Monteleone & Houde 1992; The Bahamas, various spp., Layman & Silliman 2002; temperate Australia, various spp., Edgar & Shaw 1995a, 1995b; tropical Australia, various spp., Blaber 1980, Blaber et al. 1989, Salini et al. 1990, Haywood et al. 1998, Salini et al. 1998, Chapter 3). Thus the shallow water refuge paradigm has overlooked a component of the estuarine fauna which may contribute significant mortality (Martin

& Blaber 1983) and create bottlenecks in the life history of fishes utilising these habitats (Halpern 2004, Sheaves 2005).

Early life history stages of fishes suffer massive levels of natural mortality (Sogard 1997, Webster 2002, Webster & Almany 2002). Small changes in early mortality rates can have a profound influence on ultimate cohort strength (Deegan 1993, Yanez-Arancibia et al. 1994). For example, predation on coral reef fish in the first few hours after settlement can have a significant and long-term influence on cohort survivorship and the structure of reef fish assemblages (Almany 2004, Almany & Webster 2004). Similarly, predation on new recruits to shallow estuarine nursery habitats has the potential to create a significant bottleneck which structures estuarine fish communities.

Because of the temporally patchy nature of recruitment (Robertson & Duke 1990b), the consumption of new recruits by estuarine predators must also be patchy (Nemerson & Able 2004). Dietary data on tropical/subtropical estuarine fishes are usually presented pooled over sampling occasions and locations to provide average diets (e.g. Blaber & Blaber 1980, Salini et al. 1990, Haywood et al. 1998, Salini et al. 1998, Chapter 3). 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 different predators. However, the importance of prey to the predator does not necessarily reflect the importance of the predator to particular prey. Specifically, just because minor piscivores within shallow estuarine nursery habitats may derive little of their nutrition from fish prey, it does not follow that minor piscivores that prey on new recruits are not important sources of mortality for recruiting fishes (Martin & Blaber 1983).

The low average occurrence of fish in the diet of minor piscivores could reflect consumption of alternate prey for most of the time, with occasional switches to target new recruits (e.g. Martin & Blaber 1983, Köster & Möllmann 2000, Swain & Sinclair 2000, Nemerson & Able 2004). Prey switching is defined here in a general sense to mean a change from the average diet to include a large amount of an otherwise rarely consumed prey. Detecting prey switching events in estuarine systems is a challenging task given the complex and dynamic nature of habitat use in these systems (Rozas & Minello 1997, Nemerson & Able 2004, Sheaves 2005, Rountree & Able 2006) and the difficulties this presents in sampling the fish community (Kneib 1997, Rozas & Minello 1997, Blaber 2002, Smith & Hindell 2005). Despite the challenge in detecting events such as prey switching, ignoring such events may give seriously misleading interpretations of the importance of predation in structuring these systems (Edwards et al. 1982, Martin & Blaber 1983, Swain & Sinclair 2000).

One possible approach to determine if minor piscivores switch to target new recruits would be to estimate the abundance of new recruits through time and or space, concurrently examine the diets of minor piscivores, and see if they correlate. However, this approach makes the assumption that new recruits are distributed approximately uniformly throughout the area covered by a foraging predator prior to its capture, such that the measured densities of new recruits represent the densities of new recruits available to their potential predators, and that the predators sampled have actually encountered new recruits at the density measured. If prey resources are spatially patchy at the scale of the foraging predator, then detecting prey switching events through a correlative approach may be difficult (e.g. Marchand et al. 1999, Rountree & Able 2006).

Despite the potential challenges in detecting such events, prey switching by abundant minor piscivores has the potential to exert significant mortality on fishes recruiting to shallow estuarine nurseries (Martin & Blaber 1983). The aim of this chapter was to determine if common minor piscivores switch to prey on new recruits during recruitment events in tropical estuarine systems of north-eastern Australia. To address this aim, two approaches were adopted. To look for direct evidence of prey switching in response to recruitment events, 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. Secondly, a broad view of the spatio-temporal patterns in the consumption of fish prey by minor piscivores was gained by examining the diets of minor piscivores collected from the Ross River and 16 other estuarine systems in the region between 1999 and 2004.

4.2 METHODS

4.2.1 Recruitment variability, minor piscivore diets, and prey switching. Recruit abundance and the diets of minor piscivores were monitored during 2001-02 in the Ross River estuary in north-east Queensland, Australia (Fig. 3.1), to look for direct evidence of prey switching in response to recruitment events. Samples were collected along shallow ($\leq$1.5 m) sand banks in the lower 2km of the estuary. Unvegetated sand banks are the dominant shallow-water habitat in the lower reaches of estuarine systems in this region. Initially samples were collected every 3-4 days from 27th of February 2001 until 29th of March 2001 (9 sampling occasions). From this it was determined that sampling on the full and new moons would adequately represent new recruits to the system. Subsequent sampling was conducted fortnightly on the 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.

On each occasion, five replicate 10 m hauls were made using a 12 m x 6 mm mesh seine net. Collected fish were taken to the laboratory for identification and enumeration. 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, individuals ≤20 mm are relatively new recruits (Robertson & Duke 1990b, Baker & Sheaves pers. obs.). Additional hauls using the same gear were made to supplement samples of predatory fishes for gut content analysis.

Least squares univariate classification and regression tree (CART) analysis was used to examine the occurrence of fish prey in the diets of predatory fishes in relation to recruit abundance on various sampling occasions (De'ath & Fabricius 2000). The technique successively splits the data into increasingly homogenous groups by minimising the residual sums of squares for each split, analogous to least squares regression (De'ath & Fabricius 2000). In this analysis, the 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. Each split in the tree indicates the variable which explains the most 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 indicated by the explanatory variable of 'recruit abundance' forming one or more splits on the tree whereby 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. + 1SE rules (Breiman et al. 1984).

4.2.2 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 would be equal to 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).

4.2.3 Spatio-temporal variability in fish predation by minor piscivores. In addition to the diet data from the Ross River samples, a broader view of spatio-temporal patterns in the consumption of fish prey was gained by examining the diets of minor piscivores collected from the Ross River and 16 other estuarine systems in the region between 1999 and 2004 (Fig. 3.1). Details of the sampling protocol and dietary analysis are given in Chapter 3. Briefly, predatory fish were collected for gut content analysis from shallow (≤1.5 m) sandy habitats in the lower reaches (≤5 km) of each estuary. Because of the broad and essentially unpredictable timing of fish recruitment in this region (Robertson & Duke 1990b), sampling effort was allocated as broadly as possible within the spatial and temporal limits of the study. Various gears were used to ensure a wide range of predator sizes and taxa were represented.

Minor piscivores are classified as such because of the low average occurrence of fish in their diets (Whitfield & Blaber 1978a). Spatio-temporal patterns in the diets of common minor piscivores identified in chapter 3 (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. To determine how well the average occurrence of fish in the diet represents spatial and temporal patterns in predation on fish, histograms were constructed showing the frequency of samples of minor piscivores with different levels of fish in the diet. The normal curve based on the mean and standard deviation of occurrences of fish across the samples was fitted to each histogram. The normal curve represents the expected distribution of observed occurrences of fish in the diet of minor piscivores, if the mean occurrence was representative. Poor agreement between the normal curve and the observed distribution indicates that the average occurrence of fish in the diet is a poor representation of spatio-temporal patterns of predation on fish by minor piscivores. In constructing the histograms only samples that contained ≥ 4 individuals were included. Consequently, the means and standard deviations used to calculate the normal curves represent values across samples where $n \geq 4$. As such, the means deviate slightly from the overall percentage occurrence of fish for each taxon/size class (Table 3.1). Higher than average occurrences of fish in the diet of minor piscivore taxa on particular sampling occasions were crossreferenced among all the minor piscivore taxa sampled at the same location/time to look for evidence of multiple species switching to fish prey.

4.2.4 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 (Appendix A). Otoliths showing signs of digestion were not used to estimate prey length (see Chapter 3.2.5).

4.3 RESULTS

4.3.1 Recruitment variability, minor piscivore diets, and prey switching. Recruitment was highly temporally variable, 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. 4.1). Throughout the year recruits were dominated by *Leiognathus* spp., *Secutor* spp. (Leiognathidae), *Sillago* spp. (Sillaginidae) and *Gerres* spp. (Gerreidae). The largest sample (10 599 recruits on 13th of March 2001) was primarily *Leiognathus* spp. The sample of 629 recruits on March 29th 2001 was a mixture of *Sillago* spp., *Leiognathus* spp. and *Gerres* spp., while the

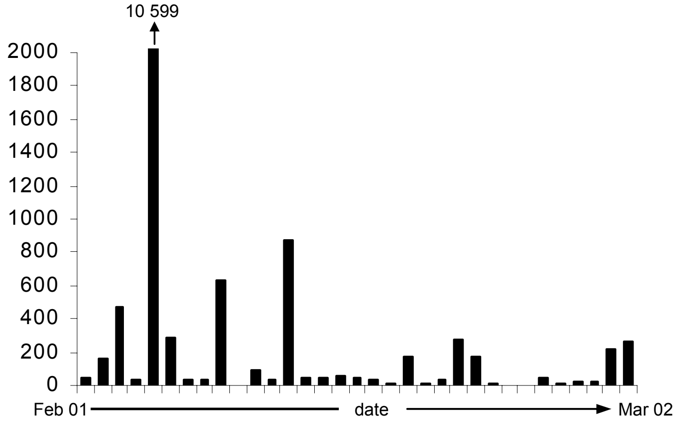


Figure 4.1: Abundance of fish ≤20 mm FL in samples from the mouth of the Ross River, February 2001-March 2002.

868 new recruits sampled on May 23rd were mainly *Sillago* spp. Details of the species composition and recruitment patterns will be published elsewhere.

A total of 501 individuals from 15 taxa of common minor piscivores were sampled from the Ross River and examined for gut contents (Table 4.1). Each of these predators generally consume benthic invertebrates or planktonic crustaceans (Wilson & Sheaves 2001, Baker & 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 relationship 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.

Table 4.1: Sample size and % occurrence of fish in the diet of minor piscivores sampled from the Ross River, Australia, 2001-02.

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

*size classes identified as minor piscivores (see Appendix C).

4.3.2 Spatial patchiness of new recruits. Spatially, new recruits were highly aggregated. On most sampling occasions the variance in abundance estimates from the 5 replicate net samples was orders of magnitude greater than the mean (Fig. 4.2, Table 4.2). On the only three occasions when the variance to mean ratio indicated the possibility of a random or uniform distribution of recruits (VMR ≤1.5), very few recruits were recorded (Table 4.2).

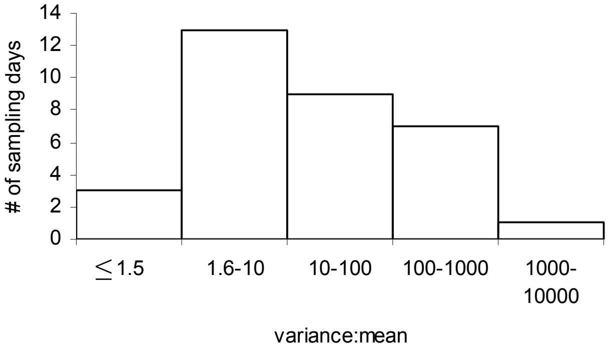


Figure 4.2: Distribution of variance to mean ratio in the abundance estimates of new recruits from 5 replicate nets on each sampling occasion, Ross River, 2001-02.

Table 4.2: 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.

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	10285	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	10599	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

4.3.3 Spatio-temporal variability in fish predation by minor piscivores. The low average occurrence of fish in the diet of minor piscivores was invariably a poor representation of spatial and temporal patterns in their consumption of fish prey (Fig. 4.3). Most of the time none or very few individuals had consumed fish prey, while

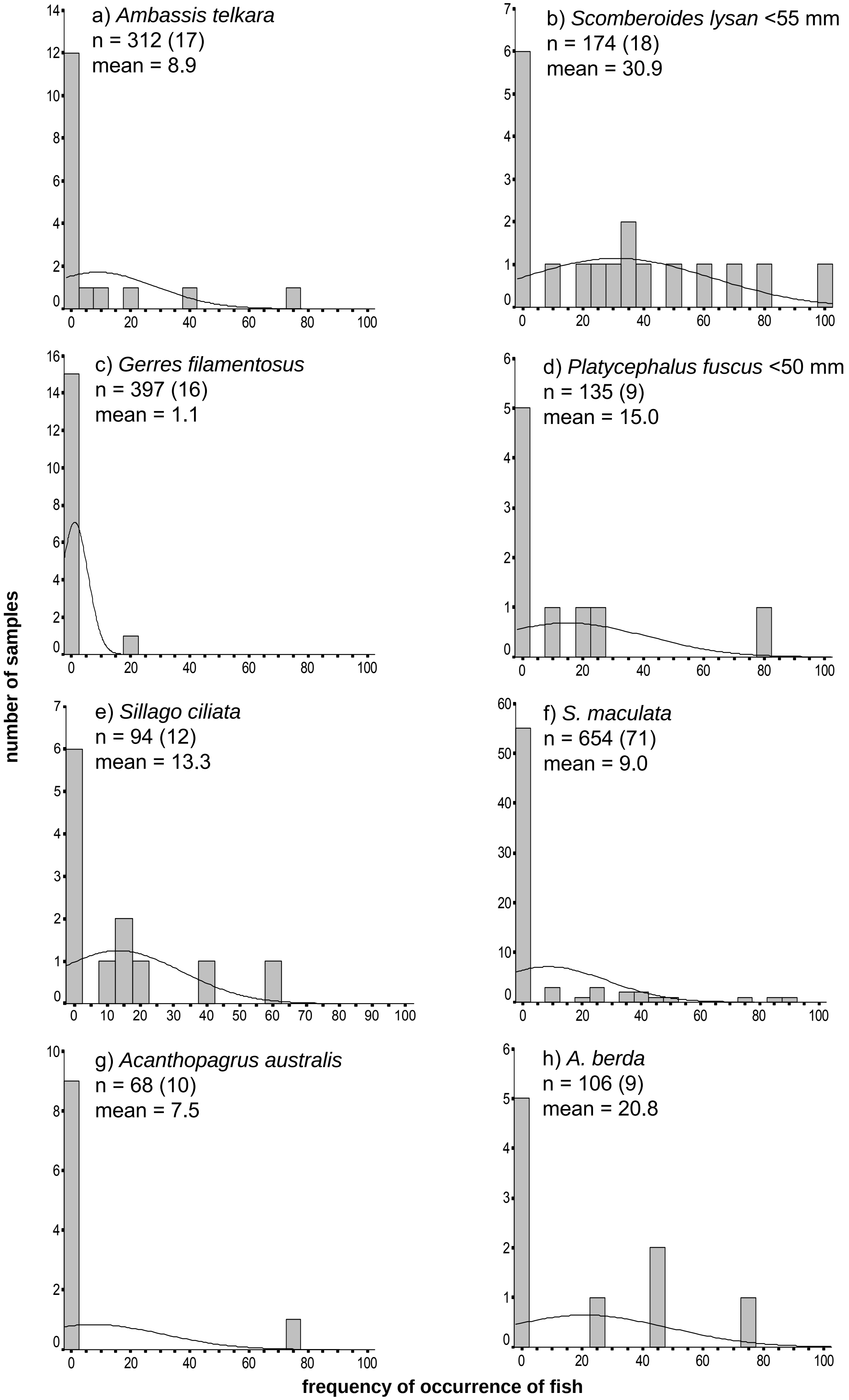


Figure 4.3: Spatio-temporal variability in the occurrence of fish in the diet of minor piscivores. Only samples where n ≥ 4 are included. Sample size, the number of samples, and the mean occurrence of fish across those samples is presented. E.g. 312 *A. telkara* came from 17 samples with n ≥ 4 and had an average occurrence of fish of 8.9 %. The normal curves are fitted based on the mean and standard deviation of the distributions.

occasionally a large proportion of individuals had done so. Within particular estuaries on certain sampling occasions, multiple species of minor piscivore had an above average occurrence of fish prey in the diet (Table 4.3). 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. In the same estuary in September 2000, of the seven species of minor piscivore examined for gut contents, six had consumed fish prey and all six had above average occurrence of fish in the diet. Other examples of multiple species consuming fish prey were observed on several occasions, including Cassidy Creek in November 2001, Ross River in May 2000, and Blacksoil Creek in November 2001 (Table 4.3). On other occasions the consumption of fish by one or few species of minor piscivore was not reflected in other members of the assemblage. For example, while one of the four *Sillago maculata* examined from Deluge Inlet in November 1999 had consumed fish, none of the other eighty-nine individuals from six taxa had consumed fish prey (Table 4.3).

When minor piscivores consumed fish prey, they preyed mainly on small new recruits (Figure 4.4). 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 figure 5 were mostly small and unidentifiable. While some unidentified fish prey may have been individuals of small species such as gobiids, common local gobiids <20 mm are also relatively new recruits (Baker & Sheaves pers. obs.).

Table 4.3: Spatio-temporal overlap in the consumption of fish prey by minor piscivores in estuaries of north-eastern Queensland, Australia. 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 piscs examined for gut contents.

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

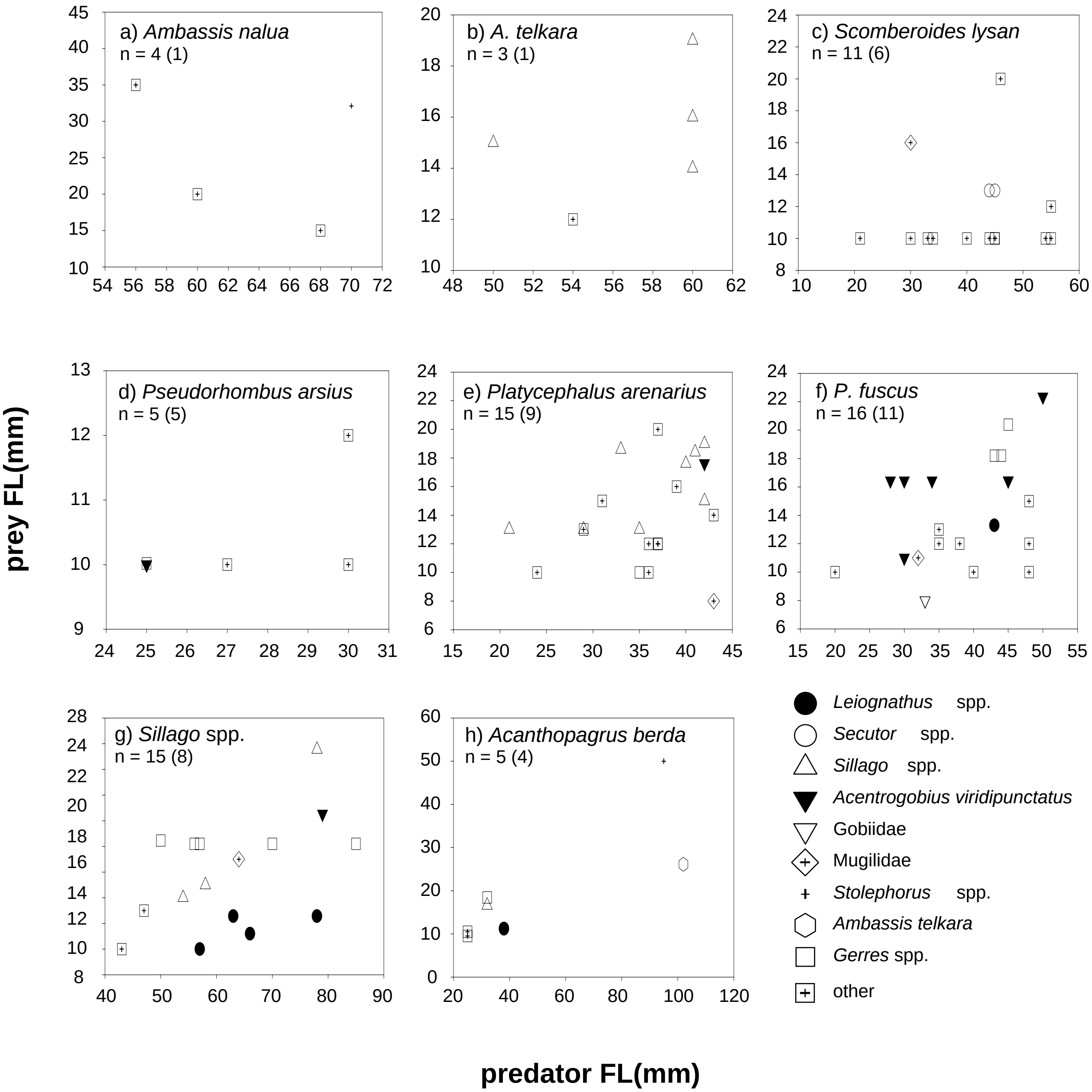


Figure 4.4: Fish prey size and identity in the diets of minor piscivores from shallow estuarine nursery habitats. The sample size and number of samples of predators in which fish prey were identified are shown, e.g. the fish prey identified in the guts of *A. telkara* came from three individuals collected from one sample.

4.4 DISCUSSION

4.4.1 Correlating abundance and diet in an inherently patchy system. There was no relationship detected between the abundance of new recruits and the occurrence of fish in the diets of minor piscivores in the Ross River during 2001-02. This indicates that either 1) the minor piscivores did not switch in response to recruitment events, or 2) they did switch but this was not detected. Given the highly aggregated distribution of recruits within the shallow water habitats sampled (Fig. 3, 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. 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 & Minello 1997, Minello & Rozas 2002, Nemerson & Able 2004, Sheaves 2005, Rountree & Able 2006). Therefore it 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). This is because in many instances patches of recruits will be sampled while the minor piscivores sampled will not have encountered recruits, even if they occur in the same replicates. On other occasions, predators which have encountered and consumed recruits will be captured, yet 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. Even though 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 six hours for fish prey to digest or pass through the stomach of small predatory fishes from estuaries in north-eastern Queensland (Baker unpub. data.). It is highly problematic to determine the area covered by a small fish inhabiting intertidal estuarine habitats over a six hour period (Rozas & Minello 1997, Sheaves 2005, Rountree & Able 2006). Furthermore, interpretations of the spatial significance of the gut contents will be confounded by the behaviours of both predator and prey upon encounters between the two (Abrams 1993, Manderson et al. 2000, Sancho 2000, Juanes et al. 2001, Turesson et al 2002, Preisser et al. 2005).

It could be argued that the failure to detect a switch by the minor piscivores within the 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 & 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 & Minello 1997, Nemerson & Able 2004, this study), it will not be possible to correlate prey abundance with predator diet (e.g. Marchand et al. 1999). Despite the challenge in directly detecting 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 suggests that minor piscivores may in fact switch from a non-fish diet to prey heavily on new recruits during recruitment events.

4.4.2 Indirect evidence of prey switching. The low average occurrence of fish in the diets of minor piscivores (Wilson & Sheaves 2001, Baker & 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, minor piscivores did not consume fish prey at all, while occasionally a large proportion of individuals did so (Fig. 4, Table 3). When they consumed fish, they preyed mainly on small new recruits (Fig. 5), which were only available in high abundance occasionally because of the temporally patchy nature of recruitment (Robertson & Duke 1990b, Fig. 2 this study). The spatial variability in recruit abundance made it difficult to correlate recruit abundance with the occurrence of fish in minor piscivore diets (e.g. Marchand et al. 1999). However, while the sample sizes of individual species of minor piscivores examined for gut contents on any particular sampling occasion may be small, multiple species of minor piscivore all preying on recruits at one place and time provides a strong indication of a switch among the minor piscivores to target recruits in response to a recruitment event (Table 3). Thus the evidence suggests that 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 & Blaber 1983).

4.4.3 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 (Blaber 1980, Robertson & Duke 1987, Salini et al. 1990, Monteleone & Houde 1992, Edgar & Shaw 1995a, Haywood et al. 1998, Wilson & Sheaves 2001, Maes et al. 2003, Hampel & Cattrijsse 2004). Consequently, alternate food sources maintain a large abundance and biomass of predatory fishes in shallow nursery habitats (Wilson & Sheaves 2001), which potentially inflict heavy mortality on new recruits when they enter the system.

The level of refuge provided by shallow nursery habitats in tropical estuaries, and elsewhere in the world, may have been considerably 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 & Blaber 1978, Blaber 1980, Salini et al. 1990). An intense pulse of predation on early life stages could play a major role in cohort survivorship and structuring estuarine fish assemblages as it does in other systems such as coral reefs (e.g. Carr & Hixon 1995, Hixon & Carr 1997, Webster 2002, Almany 2004) and pelagic waters (e.g. Ellis & Nash 1997, Köster & Möllmann 2000, Swain & Sinclair 2000).

In estuarine systems, pulse events, such as predation on new recruits, are difficult to predict and detect (Robertson & Duke 1990b, Sheaves 2005, Rountree & Able 2006). Shallow water nursery assemblages mainly utilise intertidal habitats and are thus constantly moving in response to tidal fluctuations (Rozas & Minello 1997, Nemerson & Able 2004, Sheaves 2005, Rountree & Able 2006). Because of this, abundance estimates are highly variable (Rozas & Minello 1997, Rountree & Able 2006, Table 2 this study) and monitoring changes in abundance through time to estimate mortality, as is done on coral reefs (e.g. Almany 2004), is not possible (Rountree & Able 2006). Examining gut contents of predatory fishes is one way to detect and measure predation mortality (Buckel et al. 1999, Rountree & Able 2006), however this approach is limited by the length of time it takes to digest prey (Haywood 1995, 1998). A predation event on new recruits entering an estuary on one incoming tide may inflict massive mortality (Martin & Blaber 1983) but only be detectable for a few hours following the event (Haywood 1995). 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 & Möllmann 2000, Sheaves 2005). Previously overlooked minor piscivores may be a significant component of the piscivore assemblage and the role these predators play within shallow estuarine nursery habitats is worthy of further investigation.

Chapter 5

Visual surveys reveal high densities of large piscivores in shallow estuarine nurseries

ABSTRACT

Shallow estuarine nurseries are widely believed to provide juvenile fishes with refuge from predation due to the low numbers of piscivorous fishes. Observations during several years of field work in north-eastern Australia indicate that the assemblage of large (≥100 mm) piscivorous fishes within shallow tropical estuarine nurseries may have been considerably underestimated by previous sampling efforts. This study utilised visual surveys of shallow sandy shorelines in the lower reaches of estuaries to estimate the abundance of large piscivores. Flathead (*Platycephalus* spp., Platycephalidae) were the only large piscivores sighted within the transects. A total of 296 flathead between 100 and 600 mm TL were observed in waters between 0.02 and 0.62 m deep. The density of flathead observed during the present study (0.04 ind. m^{-2}) equated to one piscivore ≥100 mm TL for every 10.5 m of shoreline surveyed, and far exceeds density estimates for large piscivores in shallow estuarine habitats elsewhere in the world. Furthermore, the estimated biomass of flathead (11.56 g m^{-2}) was equivalent to comparable biomass estimates of entire fish assemblages from shallow estuarine habitats in other parts of the world. The densities and depth distribution of these large piscivores suggests that shallow water nurseries may not provide small fishes with the level of refuge from predation previously assumed.

5.1 INTRODUCTION

Shallow estuarine habitats around the world are considered to be valuable nurseries because they are believed to provide abundant food and refuge from predation for small and juvenile fishes (eg. Blaber & Blaber 1980, McIvor & Odum 1988, Ruiz et al. 1993, Laegdsgaard & Johnson 1995, Beck et al. 2001). The refuge theory is based, in part, on reports of low abundances of piscivorous fishes within estuarine habitats (eg. Shenker & Dean 1979, Blaber 1980, Rozas & Hackney 1983, Boesch & Turner 1984, Paterson & Whitfield 2000). The piscivore assemblage of shallow (<1.5 m) tropical estuarine habitats in north-eastern Australia was recently found to be far more diverse and abundant than previously thought, with a large proportion of fishes that inhabit shallow estuarine waters being piscivorous to some degree (Ch. 3 & 4). While this expanded view of the piscivore assemblage mainly incorporates previously overlooked small and occasional piscivores that prey on new recruits, observations during several years of field work indicate that the assemblage of large piscivorous fishes within shallow tropical estuarine habitats are considerably underestimated.

Aspects of the use of shallow-water habitats by piscivorous fishes have been examined in temperate Australian estuarine systems (e.g. Hindell et al. 2000, 2001, Smith & Hindell 2005), however these studies have focussed mainly on structurally complex habitats such as seagrass beds and mangroves. The shallow water habitats utilised as nurseries in tropical north-eastern Queensland are predominantly structurally simple and unvegetated. Fishes may gain access to mangrove forest habitats during larger high tides, however for the majority of the time these habitats are inaccessible (Sheaves 2005). Although several species of seagrass occur lower in the intertidal and subtidal areas of the regions estuaries, these do not form extensive meadows common in other parts of the world (Coles et al. 1987, 1993, Hindell et al. 2000). The structural and faunal differences between tropical and temperate systems mean that processes such as habitat use and predation are likely to vary considerably between these systems (Smith & Hindell 2005).

Platycephalus spp. (Platycephalidae, mainly *P. fuscus,* also *P. endrachtensis* (*indicus*) and *P. arenarius*) were the most abundant and commonly encountered primary piscivores in shallow (<1.5 m) waters of estuaries sampled with seine nets by Baker and Sheaves (2005) (Ch. 3). The diet of large (≥100 mm) flathead (*Platycephalus* spp.) in this region primarily consists of small and juvenile fishes that utilise shallow-water nursery habitats (Ch. 3). However, large flathead are generally reported in relatively low abundances from similar habitats in this and other parts of the Indo-West Pacific (Blaber et al. 1989, Blaber & Milton 1990, Haywood et al. 1998, Salini et al. 1998, Sheaves 2001). During the course of sampling 17 estuaries over several years, large flathead were regularly seen retreating from the shallow margins of sandbanks when spooked by the net operators or boat (Baker & Sheaves pers. obs.). It is clear that these relatively common, large, shallow-water specialist piscivores (Sheaves & Molony 2000, Ch. 3) have been underrepresented in shallow waters by previous sampling efforts. The aim of this chapter was to determine the density of large piscivores (≥100 mm) in shallow water habitats.

5.2 METHODS

5.2.1 Study sites and field methods. The density of large (≥100 mm) piscivores in shallow tropical estuarine waters was estimated by visual census. Between July 2003 and August 2004, 39 transects were surveyed by walking the shore line along shallow, unvegetated sand banks in the lower reaches (<5 km) of four estuaries in north-eastern Queensland, Australia (Victoria Creek n = 12, Herbert River n = 20, Seymour River n = 6, and Ross River n = 1, Fig. 3.1). Transects were between 10 and 1300 m long (av. ± SE = 232 ± 33 m, total 9036 m) and between 1 and 5 m wide (35 were 3 m wide) depending on the topography of the shore. The methodology was primarily designed to measure the density of large (≥100 mm) flathead (*Platycephalus* spp.), and during the course of the study no other large piscivores were sighted within the transects.

Flathead bury themselves into the substrate from where they ambush passing prey (Douglas & Lanzing 1981). Their behaviour makes them particularly amenable to visual census in shallow waters. They generally remain buried until the observer approaches within a few metres, and upon spooking they retreat into deeper water in a direction approximately perpendicular to the shore. Retreating flathead leave an imprint or ‘lie’ in the substrate (Fig. 5.1). Occasionally, imprints of the pectoral and caudal fins are visible within the lies, and observations of these indicate that the total length of the flathead can be accurately estimated from the length of the lie. Most transects were censused a second time, immediately following the initial census, by walking back along

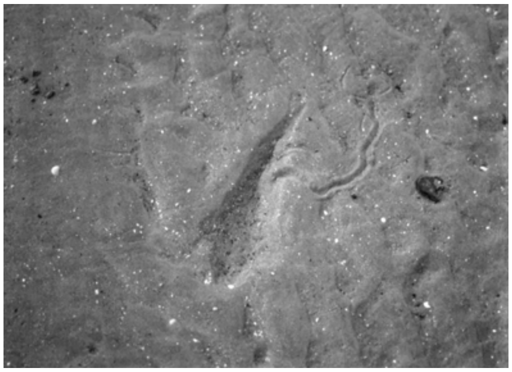


Figure 5.1: The imprint or ‘lie’ of a flathead (*Platycephalus* spp.) left on an intertidal sandbank.

the shoreline just surveyed. The second census revealed only two flathead during the entire study, indicating that spooked flathead rarely returned to the transect within the time frame of the initial census. Additionally, the within-transect density patterns observed provide no evidence of the observer ‘herding’ flathead along the shore. Consequently, the probability of an individual flathead being observed and counted more than once during any census was low.

Density was estimated by counting the number of individuals observed within each transect. The distance of each individual along a transect was measured (± 1 m) using a distance measuring wheel. The size of individual flathead was measured as the length of the lie (± 2.5 cm) left by fish observed retreating into deeper water, and the depth at which the flathead was stationed was measured as the depth at the head end of the lie (± 1 cm). When a flathead was observed near the outer edge of the predefined transect (see below for determination of transect widths) the distance of the lie from the shore was measured. Only individuals confirmed to have been stationed within the predefined transect were recorded. Only lies left by observed fish were measured. Lies left by individuals that were not observed were not measured because an actively feeding individual could leave multiple lies within an area.

Particular shoreline characteristics and conditions are required to successfully conduct visual surveys within estuaries. The water must be clear enough to see the bottom beyond the outer edge of the transect. Rough weather, wind, large tides and muddy substrate create turbid water or ruffle the water surface making many sites or occasions unsuitable for visual surveys. The sediment within the transect must retain imprints or lies that are clear enough to gain accurate length estimates. Cloud cover and the position of the sun also influence visibility within the transect. Compounding visibility issues, the presence of estuarine crocodiles in many of the estuaries in the region made entering the water to measure size and depth of flathead too dangerous at many locations where flathead were regularly observed.

In an effort to ensure reliable density estimates, transect widths were set prior to the commencement of each survey based on the visibility conditions at the beginning of the transect. Widths were set such that a flathead that was spooked at least 1 m beyond the outer edge would be clearly visible, ensuring that all fish spooked within the defined transect would be observed. However, variable visibility along the length of many transects, caused by changes in topography, turbidity, wind direction or cloud cover, meant that density estimates from some transects were considered unreliable due to poor visibility. For each transect surveyed, visibility was categorised as either ‘good’ or ‘poor’. A rating of ‘good’ indicated that visibility was consistent along the length of the transect, such that the observer was confident of spooking and sighting fish at least 1 m beyond the outer edge for the entire length of the transect. ‘Poor’ visibility meant that because of variable visibility conditions along the transect, some spooked fish might not be sighted or that fish within some sections of the transect may not have been spooked by the passing observer.

5.2.2 Analysis. Only data from the transects classified as having good visibility were included in analyses. The density of flathead (individuals m^{-2}) within each transect was calculated. Biomass estimates were derived from the length-weight relationship of *Platycephalus fuscus* 100-442 mm TL (n = 75), the most abundant *Platycephalus* spp. sampled from these habitats (Ch. 3). The length-weight relationship is described by the equation $weight(g)=0.0000027 \times length(mm)^{3.1421}$, $r^2 = 0.997$. This equation was used to estimate the weight of all flathead observed, including the 29 individuals >442 mm TL. Although it is potentially inaccurate to extrapolate estimates beyond the range of data used to calculate the length-weight relationship, the high r^2 for the relationship indicates that the weight estimates for those individuals up to the maximum length recorded (600 mm TL) should be reasonably accurate.

Because flathead appeared to form aggregations, the 10 m maximum density was calculated (the maximum density of flathead within a 10 m long section of the transect). The null hypothesis that flathead were randomly distributed within the transects (i.e. not aggregated) was tested using a Chi-squared goodness-of-fit test (Zar 1999). To achieve this, each transect was treated as a series of 3 x 3 m quadrats. The observed frequency distribution of the number of flathead per quadrat was compared to the expected frequency given a Poisson (random) distribution. To determine any size-related pattern in the minimum water depth occupied by flathead, the slope of the lower boundary of the relationship between flathead size and water depth was estimated using quantile regression (Scharf et al. 1998a). The significance of the slope estimate was determined using the bootstrap resampling technique of Gould (1992). The relative abundance (% of total) of flathead occupying each 100 mm depth zone within each transect was calculated. To determine the depth distribution of flathead within transects, the average relative abundance in each depth zone was calculated for the transects with good visibility in which 10 or more individuals were sighted (n = 9 transects).

5.3 RESULTS

A total of 296 flathead ≥100 mm TL were observed. Of these, 281 were sighted in the 14 transects classified as having good visibility. Only these 14 transects were used to estimate densities and biomass, and these transects were each 3 m wide. No large individuals (>100 mm) of other piscivorous taxa were sighted in any transect. Up to 71 flathead were sighted within a single transect (Fig. 5.2c). The average density (± SE) was 0.0428 ± 0.0139 m^{-2} (range 0.0027 to 0.1972 m^{-2}) (Table 5.1). This equates to an average of one flathead ≥100 mm TL for every 10.5 m of shoreline surveyed. Average biomass (± SE) was 11.56 ± 3.72 g m^{-2}, ranging from 0.12 to 46.16 g m^{-2}.

Flathead were significantly aggregated (Chi-square (2 d.f.) = 448.8, p<0.001, variance:mean = 3.3:1). Larger aggregations generally spanned much of the observed depth range within each transect (Fig. 5.2). Five or more individuals were found within 10 m sections in nine transects (e.g. Fig. 5.2a), and 10 m maximum densities were up to 0.8667 m^{-2} (26 fish within a 10 x 3 m section of shoreline) (Table 5.1, Fig. 5.2c).

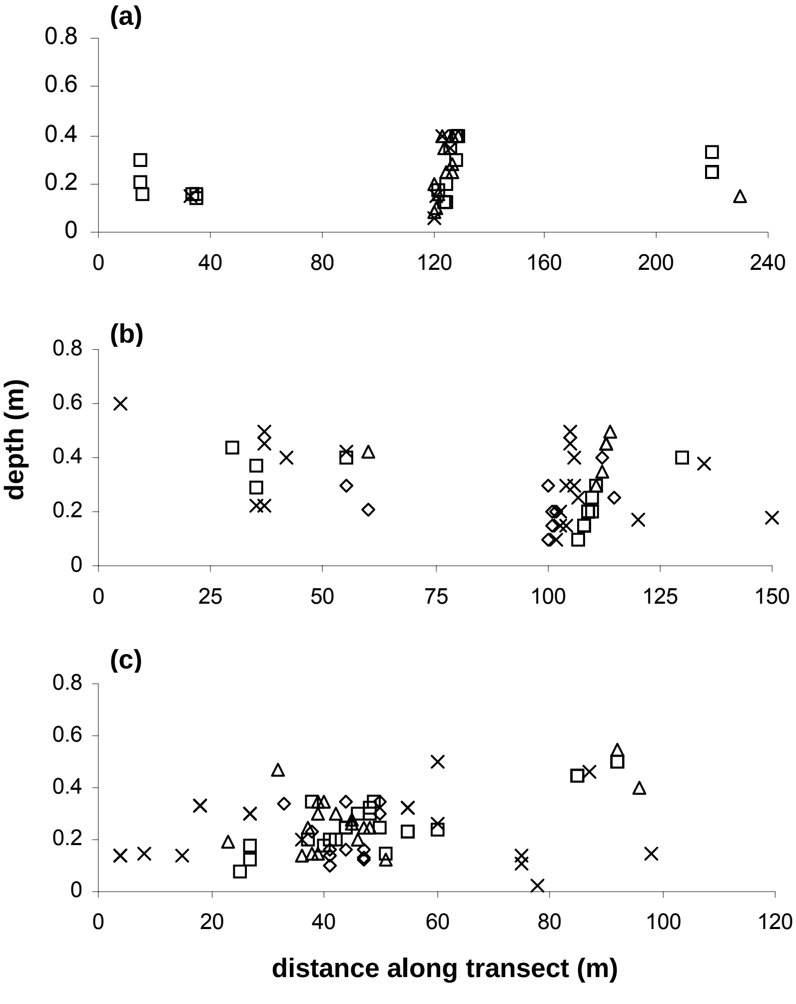


Figure 5.2: Examples of the size structure and depth distribution of flathead (*Platycephalus* spp.) observed during visual census of shallow sandy shores in the lower reaches of Victoria Creek. TL mm: x = 100-200, box = 201-300, triangle = 301-400, diamond = 401-500. Shown are data from 3 transects; a) 12/11/03b, b) 6/1/04a, and c) 30/1/04b.

Often, more than one aggregation of 5 or more individuals would be present within a transect (e.g. Fig. 5.2b, c).

Some large flathead were observed in very shallow water (Fig. 5.3). The flathead sighted ranged in length from 100 to 600 mm TL and were stationed in waters between 0.02 and 0.62 m deep (Table 5.1, Fig. 5.3). Although there is some indication of smaller fish entering slightly shallower waters than larger individuals (Fig. 5.3), the slopes of quantile regressions describing the lower boundary of the flathead size-water depth distribution were not significant for any of the 1st, 5th or 10th quantiles. This means there was no significant relationship between flathead size and the minimum water depth occupied among the individuals surveyed.

Table 5.1: Density, size and depth distribution of *Platycephalus* spp. along shallow sandy habitats in the lower reaches of tropical estuaries in north-eastern Australia, as determined by visual census. 10 m max. density is the maximum density observed within a 10 m section of the transect. Actual number of individuals observed in the density maximum is shown in parenthesis.

Location	Date code	Transect length (m)	Area (m^2)	# flathead	Density ($\#m^{-2}$)	Biomass (gm^{-2})	10m max. density (n)	TL(mm) range	Depth range (m)
Ross	240703a	10	30	1	0.0333	36.71	0.0330 (1)	550	0.04
Victoria	121103a	375	1125	24	0.0213	5.80	0.3000 (9)	100-500	0.04-0.50
Victoria	121103b	240	720	34	0.0472	8.25	0.7667 (23)	120-400	0.06-0.40
Victoria	060104a	150	450	48	0.1067	22.78	0.6667 (20)	130-500	0.10-0.60
Victoria	060104b	200	600	17	0.0283	4.67	0.1667 (5)	180-400	0.17-0.60
Victoria	060104c	130	390	13	0.0333	7.61	0.2000 (6)	160-420	0.20-0.60
Victoria	300104a	120	360	18	0.0500	8.13	0.2000 (6)	140-420	0.08-0.58
Victoria	300104b	120	360	71	0.1972	46.16	0.8667 (26)	140-500	0.02-0.55
Herbert	280504a	250	750	2	0.0027	0.12	0.0330 (1)	200-200	0.08-0.12
Herbert	280504b	131	393	5	0.0127	5.98	0.1000 (3)	160-550	0.10-0.50
Herbert	140704h	416	1248	11	0.0088	2.60	0.1667 (5)	180-570	0.05-0.30
Herbert	140704i	250	750	4	0.0053	0.59	0.0667 (2)	100-350	0.03-0.40
Victoria	150704a	185	555	25	0.0450	9.89	0.2333 (7)	200-450	0.20-0.62
Herbert	120804e	386	1158	8	0.0069	2.53	0.1000 (3)	250-600	0.10-0.30
total (average)	39 transects	9036		296	(0.0428)	(11.56)		100-600	0.02-0.62

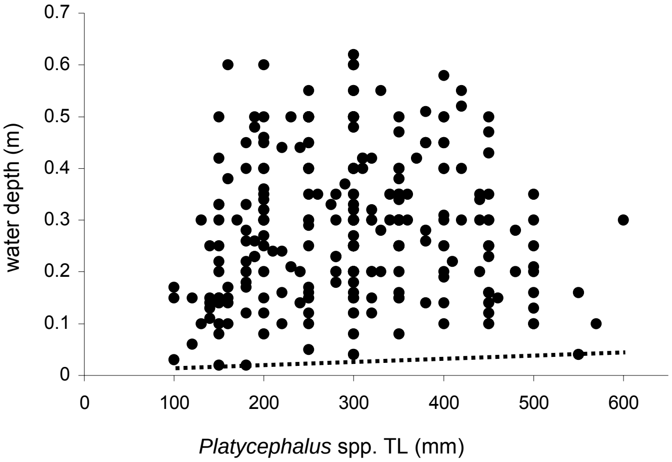


Figure 5.3: Size-related depth distribution of flathead (*Platycephalus* spp.) (n = 296) along shallow sandy banks in the lower reaches of tropical estuaries. Dotted line represents 99th quantile of predator size - prey body depth relationship for *P. fuscus* (adapted from Ch. 3). A dot on the line indicates a predator in water of depth equal to the body depth of the largest prey eaten.

The shallowest individuals were stationed in water approximately equal to the body depth of the largest prey they could consume (Fig. 5.3). To relate the minimum observed depth of flathead to their prey, the predator length-prey length relationship for *Platycephalus fuscus* determined in chapter 3 (Baker and Sheaves 2005) was converted to a predator length-prey body depth relationship for the three deepest-bodied taxa, *Leiognathus* spp., *Ambassis telkara* and *Gerres filamentosus*. By using the deepest-bodied prey taxa, the upper boundary of the relationship (99^{th} quantile regression; Scharf et al. 1998a) indicates the maximum body depth of prey consumed across the size range of flathead. When superimposed onto the flathead depth distribution (dotted line - Fig. 5.3), it can be seen that flathead can access water as shallow as the body depth of the largest prey they could consume.

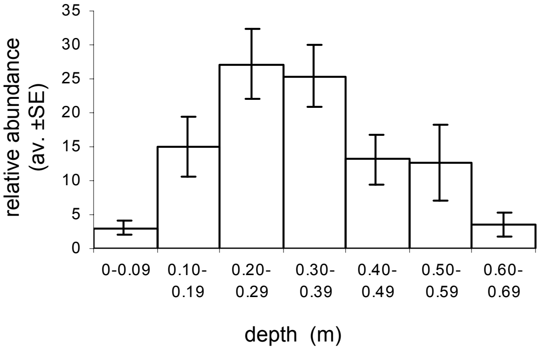


Figure 5.4: Depth distribution of flathead (*Platycephalus* spp.) ≥100 mm TL observed during visual surveys along shallow sandy shores in tropical estuaries of north-eastern Australia. Includes only transects in which ≥10 individuals were sighted (n = 9).

On average (based on the 9 transects in which ≥10 flathead were sighted), the greatest densities of flathead were stationed in water between 0.2-0.4 m deep (Fig. 5.4). For one transect the greatest density was sighted between 0.4 and 0.5 m depth, and in another it was between 0.5 and 0.6 m depth indicating that the density maximum in <0.4 m of water was not due to observer bias under-representing fish in deeper waters.

5.4 DISCUSSION

Only 14 of the 39 transects were considered reliable for providing quantitative density estimates, and only one group of piscivores were found in the transects. Despite this, the high densities and biomasses recorded suggest the densities and biomasses of large (≥100 mm) piscivorous fishes in shallow tropical estuarine habitats may previously have been underestimated by up to several orders of magnitude. The minimum transect-specific density (0.0027 m^{-2}) was approximately equal to the maximum density of flathead reported from seine net samples encompassing the same estuaries (0.0029 m^{-2} - Sheaves 2001), while the maximum density in this study (0.1972 m^{-2}) was two orders of magnitude greater than that from seine net samples. Furthermore, the number of flathead seen in 10 m sections of several transects during the present study (≥20 individuals) exceeds the total sample size of *Platycephalus* spp. reported from other tropical Indo-West Pacific estuaries sampled using a range of gears including seine nets, gill nets and beam trawls (Blaber et al. 1989, Blaber & Milton 1990, Haywood et al. 1998, Salini et al. 1998).

The maximum density (0.1972 ind. m^{-2}) and average biomass (11.56 g m^{-2}) estimates of large flathead in shallow waters in this study are equivalent to estimates of entire fish assemblages gained from block netting shallow water estuarine habitats around the world (Table 5.2). While the average density observed in the present study (0.0435 ind. m^{-2}) is one or two orders of magnitude lower than the densities listed in Table 5.2, the other studies sampled entire fish assemblages covering many trophic groups, while the present study estimated density of only one group of large piscivores. For example, Morton (1990) reported average densities and biomass of 0.27 ind. m^{-2} and 25.3 g m^{-2} for the fish assemblage of intertidal mangrove habitat in subtropical Moreton Bay, Australia (Table 5.2). This is amongst the highest recorded biomass of teleost fishes for estuarine habitats (Morton 1990, Barletta et al. 2003) and comprises an assemblage of at least 40 spp. Given that the combined top-level predators (5 spp.) collected by Morton (1990) contributed 0.002 ind. m^{-2} and 0.3 g m^{-2} to the total sample, the average density and biomass of top-level predators observed in shallow waters during the present study are very high by global standards (Table 5.2).

The common prey fishes consumed by *Platycephalus* spp. (Ch. 3) have a strong affinity for waters less than 0.75 m deep (Fig. 6.2, R. Johnston unpublished data). Fresh prey fish in the stomachs of flathead collected throughout the day from these shallow habitats (Ch. 3) suggests that flathead feed actively in these habitats during daylight hours. The minimum depth occupied by flathead is equivalent to the body depth of the largest prey

Table 5.2: Density and biomass estimates of fish assemblages of shallow estuarine habitats sampled with block nets or visual census. Table adapted from Barletta et al. (2003) and Morton (1990).

Location	Habitat	Sampling gear	# spp.	Density (ind. m^{-2})	Biomass (g m^{-2})	Source
Australia						
north Queensland (QLD)	shallow sandy shore	visual census	≤3	0.04	11.6	this study
north QLD - Embley Estuary	intertidal creek	block net and rotenone	66	-	8.2	Blaber et al. (1989)
SE QLD - Moreton Bay – total	mangrove forest	block net	40	0.27	25.3	Morton (1990)
- piscivores	mangrove forest	block net	5	0.002	0.3	Morton (1990)
New South Wales	tidal creek	block net	46	0.94	6.4	Bell et al. (1984)
Solomon Islands	intertidal creeks and forest?	block net and rotenone	85	-	11.6	Blaber & Milton (1990)
North Brazil						
Caete Estuary	tidal creek	block net	49	0.11	2.1	Barletta et al. (2003)
USA						
Florida - Everglades	prop root/mangrove forest	block net	64	8.0	15.0	Thayer et al. (1987)
Africa						
South Africa	intertidal marsh	block net	41	1.5	2.4	Paterson & Whitfield (1996)

consumed (Fig. 5.3). These shallowest-stationed flathead were generally within 1-10 cm of the shoreline. While the observed depth distribution of flathead is unlikely to be directly related to the body depth of the prey fishes examined, it is clear that the largest prey consumed by flathead can not physically access waters shallow enough to exclude their flathead predators. Furthermore, it seems unlikely that the narrow strip of shallow water between the shallowest flathead and the shoreline would provide a useful refuge habitat for smaller fishes, as few estuarine fishes in the region utilise this extreme edge habitat (Fig. 6.2, R. Johnston unpublished data).

Platycephalus spp. are just one group of a diverse piscivore assemblage recorded from shallow estuarine nurseries (Ch. 3 & 4) and the depth distribution of these alone does not determine the predation potential within these habitats. The flounder, *Pseudorhombus arsius* (Pleuronectidae), is another common shallow-water specialist piscivore (Ch. 3, Sheaves 2006). The lack of sightings of *P. arsius* during visual surveys is probably because individuals either do not spook as easily or are not as visible when spooked as flathead, rather than an indication of their absence from shallow waters. Similarly, carangids >100 mm are commonly captured when angling in these areas (Ch. 3) but none were observed in the transects. On coral reefs, during occasional, brief visits mobile carangids exert predation mortality equal to or greater than resident piscivores on other reef fishes (Hixon & Carr 1997). Although not sighted within the transects, our observations and those of other authors (Blaber et al. 1985) show larger mobile predators periodically enter shallow waters to feed, exhibiting a similar pattern of predation to that on coral reefs. Such predation events by mobile predators may be unpredictable and irregular (Hixon & Carr 1997), but assuming they are insignificant may lead to erroneous or overly simplified conclusions about the importance of predation in structuring these communities (Edwards et al. 1982).

The spatial extent of the present study is limited, with most of the successful transects conducted at Victoria Creek (n = 8) and Herbert River (n = 5) (Table 5.1). I suggest however, that similar densities of flathead occur in such habitats throughout the region. Large numbers of flathead were regularly seen in transects where poor visibility precluded formal density estimates. Additionally, densities of *Platycephalus* spp. in seine net samples from 8 nearby estuaries were consistently comparable to or greater than those recorded in seine nets from Victoria Creek (Sheaves 2006). Unfortunately, the risk of attack by crocodiles made the collection of quantitative data difficult at many locations.

The present study suggests that a significant component of the predator assemblage in shallow tropical estuarine habitats may previously have been considerably underestimated due to sampling biases. A similar conclusion was made for a well studied New Jersey (USA) estuary when a novel sampling approach (night-time sampling) was employed (Rountree and Able 1997). This led to the hypothesis that shallow water habitats in Mid-Atlantic Bight estuaries, and elsewhere in the world, may not provide young-of-the-year fishes with the level of predator refuge previously assumed.

Even with information on the abundance of piscivores, the relative refuge value of shallow water habitats remains unclear because few studies (including this one) have been able to examine the abundance of piscivores in shallow and adjacent deeper habitats in a comparable way. Furthermore, the relative density of predators in various habitats does not necessarily reflect predation pressure (Abrams 1993, Sheaves 2001). Ultimately comparisons of the relative predation pressure across the depth range are needed to address the shallow water refuge hypothesis.

Chapter 6

Do shallow tropical estuarine nurseries provide small fishes with a refuge from predation?

ABSTRACT

The shallow-water refuge paradigm has been globally applied to help explain the high abundances of juvenile fishes that utilise shallow-water estuarine nursery habitats. Despite its wide application and acceptance, there is little direct evidence indicating small juvenile fishes benefit from reduced predation pressure in shallow water habitats relative to adjacent deeper waters. This study employed chronographic tethering experiments to examine patterns in predation potential across a depth gradient (0.2 – 3 m) in the lower reaches of a tropical estuary. Over 6 months 17 replicate experimental trials were conducted, deploying a total of 183 tethered fish prey. Despite the clear and consistent patterns found in previous studies, there was no evidence of lower predation pressure in the shallow relative to the adjacent deeper estuarine waters. Given the complexity and diversity of the piscivore assemblage it is hardly surprising that no clear patterns emerged. The findings suggest that the shallow-water refuge paradigm may be too simplistic for diverse and complex tropical estuarine nursery grounds.

6.1 INTRODUCTION

The redefining of the piscivore assemblage of shallow tropical estuarine nursery habitats has identified a diverse assemblage of predators including many small and occasional piscivores whose importance has previously been overlooked (Chapters 3 & 4). This suggests that predation may inflict significant mortality on recruiting fish, and play a major role in structuring estuarine fish assemblages and in the functioning of shallow water nurseries. Despite the insights gained in previous chapters, like most previous work, they have not directly addressed one of the fundamental paradigms of estuarine nursery ground ecology; that shallow water habitats in estuaries provide vulnerable fishes with a refuge from predation. The shallow water refuge paradigm is applied globally (e.g. Blaber & Blaber 1980, Boesch & Turner 1984, Paterson & Whitfield 2000), but direct evidence that shallow waters actually reduces predation induced mortality relative to adjacent deeper habitats is sparse (McIvor & Odum 1988, Ruiz et al. 1993, Clark et al. 2003, Manderson et al. 2004).

The potential refuge value of shallow estuarine nurseries for fishes has usually been inferred indirectly from patterns of habitat use by juveniles and/or piscivores (Cain & Dean 1976, Blaber & Blaber 1980, Robertson & Duke 1987, Paterson & Whitfield 2000). Observations of high densities of small juveniles and low numbers of large, primarily piscivorous fishes in shallow habitats has led to the conclusion that predation pressure is lower in shallow than in adjacent deeper waters and thus that shallow waters provide refuge (Cain & Dean 1976, Shenker & Dean 1979, Blaber 1980, Blaber & Blaber 1980, Ronnback et al. 1999, Paterson & Whitfield 2000). The finding of an extensive (relative to previous views) piscivore assemblage that may inflict considerable mortality (Ch. 3 & 4) does not clarify and certainly does not refute the shallow-water refuge hypothesis. This is because, like most previous work, the piscivore assemblage of adjacent deeper habitats could not be sampled in a comparable manner, making any conclusions about the relative abundance of piscivores in shallow waters ambiguous (e.g. Shenker & Dean 1979, Ronnback et al. 1999). There is also evidence that the abundance of larger piscivores (>100mm) may have been considerably underestimated in shallow waters due to sampling biases (Rountree & Able 1993, Rountree & Able 1997, Chapter 5 this study). Furthermore, the relative abundance of piscivores in adjacent habitats does not necessarily reflect relative predation pressure because individual predators may not feed equally in all habitats they occupy (Abrams 1993, Haywood & Pendrey 1996, Sheaves 2001).

The most direct evidence of reduced predation pressure in shallow estuarine waters relative to adjacent deeper waters has come from tethering experiments in temperate estuaries (McIvor & Odum 1988, Ruiz et al. 1993, Clark et al. 2003, Manderson et al. 2004). Higher relative predation rates on small fish and mobile crustaceans tethered in deep water than in adjacent shallow waters provides support for the shallow water refuge hypothesis. Although tethering experiments are not without their problems (Peterson & Black 1994, Kneib & Scheele 2000), all techniques applied to sampling estuarine fish faunas have their limitations which must be considered when interpreting results (Boesch & Turner 1984, Aronson & Heck 1995, Kneib 1997, Rozas & Minello 1997).

Perhaps the most serious issue confronting the interpretation of tethering experiments is the potential for interaction between experimental artefacts and treatments (Peterson & Black 1994, Kneib & Scheele 2000, Haywood et al. 2003). Tethering experiments can only measure relative predation pressure, or predation potential (Aronson & Heck 1995), rather than absolute predation pressure because of the artefact of altered vulnerability of tethered prey relative to non-tethered prey (Barbeau & Scheibling 1994, Zimmer_Faust et al. 1994, Curran & Able 1998, Manderson et al. 2004). The effect of tethering on prey vulnerability is assumed to be constant across all treatments and therefore the measured patterns of predation potential are assumed to reflect patterns in actual predation pressure among treatments, thus providing meaningful interpretations (Aronson & Heck 1995). However, if the effects of tethering on measured predation pressure interact with treatment, the measured pattern of predation potential will be confounded and potentially meaningless (Peterson & Black 1994, Kneib & Scheele 2000). For example, tethered prey may become vulnerable to predators that normally do not consume non-tethered prey, and these predators may exert different predation pressure among treatments. In such cases, the measured patterns of predation potential across treatments may bear little resemblance to the actual patterns in predation pressure on untethered prey (Haywood et al. 2003). Such confounding is most likely to be a problem when the composition of the predator assemblage differs considerably between treatments (Peterson & Black 1994), such as may occur when comparing predation potential between vegetated and unvegetated habitats (e.g. Heck & Wilson 1987, Haywood et al. 2003). Comparisons of adjacent simple habitats differing only in depth are less likely to cause confounding interactions (Manderson et al. 2004). With due consideration given to, and attempts to overcome the limitations of the technique, tethering experiments provide one of the few direct approaches to quantifying relative predation pressure between habitats within dynamic estuarine ecosystems (Aronson & Heck 1995, Aronson et al. 2001, Rountree & Able 2006).

The present study aimed to directly determine if the shallow waters inhabited by small fishes in tropical estuaries provides them with a refuge from predation. To achieve this aim, chronographic tethering experiments were used to examine patterns of predation potential across a depth gradient in a tropical estuary. Efforts were made to overcome problems identified with previous tethering experiments (see 6.2.3 Field methodology and justification).

6.2 METHODS

6.2.1 Study sites. Chronographic tethering devices were used to examine depth-related patterns in predation pressure. Between 22nd of August 2003 and 30th of January 2004, sixteen tethering trials were conducted at Victoria Creek (18°38'S, 146°20'E), approximately 100 km north-west of Townsville, Australia (Fig. 3.1). Thirteen of the trials were conducted during daylight hours, and three trials were run at night. This estuary was chosen because there were numerous suitable sites in its lower reaches, and because it was easily accessible for night time sampling. An initial trial using 6 chronographs was run in the Ross River, Townsville (Fig 3.1) on 24th of July 2003, however, chronographs set >2 m deep at low tide were by necessity in the middle of the shipping channel, making this an unsuitable site for further experimental trials. The maximum tidal range in this region is approximately 4 m.

Each experimental site consisted of an area approximately 200 m long x 100 m wide, with sandy substrate gently sloping from straight, featureless shoreline into >2.5 m of water. Consequently, chronographs set in 2.5-3 m of water were between 50 and 100 m from the shore. Although some sites were adjacent to mangroves and/or marsh vegetation higher in the intertidal zone, each experimental trial was timed such that the tide was below any vegetation for the duration of the experiment. Therefore each site consisted of unstructured, non-vegetated essentially homogenous sandy habitat, varying only in depth along a gradient perpendicular to the shore. These site characteristics were chosen as they allowed, as far as is practically possible, the separation of the effect of depth on predation pressure from all other observable habitat variables such as the presence of vegetation or woody debris and variations in shoreline structure. Similarly, it was assumed that the effect of tethering on prey vulnerability was constant across the depth range sampled because the treatments differed only in depth, minimising the probability of an interaction between treatment and the vulnerability of tethered prey (Manderson et al. 2004). Sites were chosen where boat traffic was low to minimise disturbance during experimental trials.

6.2.2 Chronograph design. A chronographic tether is a device that allows the measurement of survival time of tethered prey (Minello 1993). The devices used in this study consisted of a waterproof plastic container housing a clock, battery and one half of a magnetic reed switch, secured to a weighted PVC base (Fig 6.1). Attached to the base

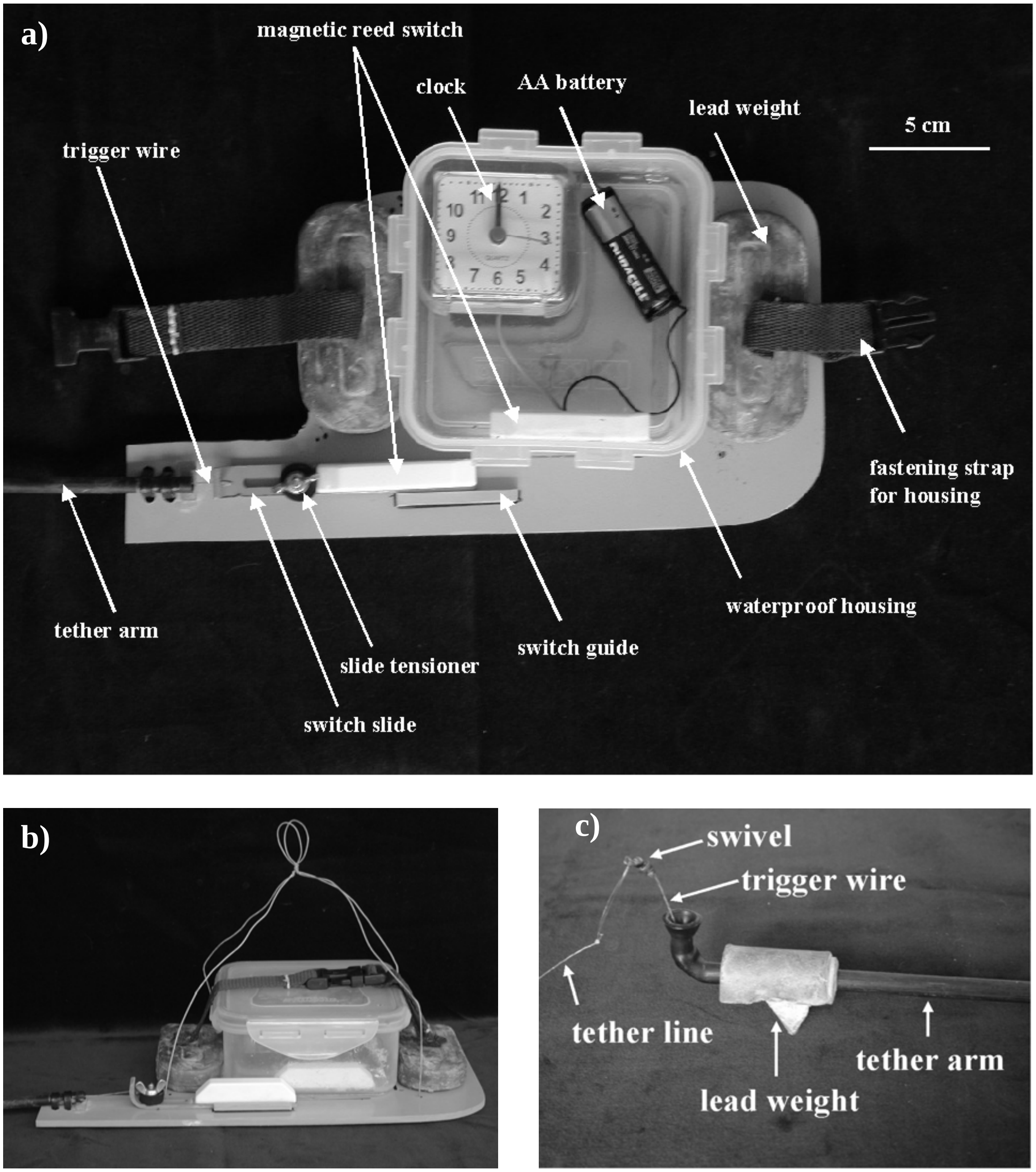


Figure 6.1: Chronograph: a) components of the chronograph showing the reed switch disengaged as it would be after a predation event, b) the closed housing fastened to the PVC base with the reed switch engaged and the clock running. The wire frame is for attachment of the float line, c) end of the tether arm (total length 35cm). The lead weight on the tether arm ensures equal triggering efficiency regardless of the direction of pull on the tether line. The trigger wire is attached to the monofilament tether line via a swivel.

was a triggering mechanism, consisting of a thin trigger wire joining the tether to the outer half of the reed switch/switch slide. The force required to trigger the switch could be adjusted by tightening or loosening a wing nut/neoprene slide tensioner on the switch slide (Fig. 6.1a). Fish were attached to the trigger wire by a tether of 35 cm of 2.7 kg monofilament fishing line (0.23 mm diam.) passed through a small hole pierced through the membrane behind the lower jaw of the fish (Fig. 6.1c). Before deployment, the tethered fish was placed into a bucket of water to ensure the tether was secure and the fish was swimming strongly. Initial trials indicated this attachment method allowed normal swimming by the tethered fish. Tethered prey also exhibited typical escape responses. For example, tethered *Sillago* spp. would often bury into the substrate when spooked, a normal escape response of these species (Baker pers. obs.).

To set each chronograph, the clock was set to 00:00 and the external section of the magnetic reed switch slid back to engage and complete the circuit, thus starting the clock (Fig. 6.1b). When a fish was eaten the tether line was pulled, sliding the switch forwards, breaking the circuit, stopping the clock, and recording survival time. Each chronograph was deployed and retrieved by a 3.5 m length of 30 kg monofilament fishing line, with one end attached to the wire frame on the chronograph (Fig. 6.1b) by a snap swivel, and the other to a 15 cm diameter styrofoam float.

6.2.3 Field methodology and justification. Within each site, between 9 and 12 chronographs were deployed across the depth range between 0.2 and 3 m. Individual chronographs were set at least 20 m apart to ensure independence of each predation event. It was assumed that a predator consuming a prey tethered to one chronograph would not be able to detect the next nearest tethered prey, and therefore each predation event could be considered independent.

The depth range sampled was chosen based on the depth distribution of common small prey fishes from the region. A range of small and juvenile fishes (<100 mm FL) that are common prey in the diets of estuarine piscivores in north-eastern Australia (Ch. 3 & 4) show both maximum densities and highest probability of encounter in waters less than 1 m deep, with very few individuals encountered in waters >1.5 m deep (Fig. 6.2; R Johnston PhD thesis in prep). Thus the depth range sampled (0.2 – 3 m) spans from the shallow waters in which small prey fish are most commonly encountered and most abundant, into the adjacent deeper waters from which they are virtually absent. While a number of taxa were tethered throughout the study, only similar sized individuals of one taxon were used in each experimental trial (Table 6.1). Prey fish used in each trial were collected with a 6 mm mesh seine net from the estuary on the day of each experiment. The taxon used was the most abundant common forage fish sampled on each occasion.

Each experimental trial was run for 2-3 hours. Although longer sets may have provided higher incidences of prey consumption (e.g. Minello 1993, Haywood & Pendrey 1996), the large tidal range meant that chronographs set in <0.5 m of water would either be in water >0.5 m or dry on the shore before the end of the trial period. In an effort to ensure representative and controlled sampling of each depth zone, experimental trials were run across the turn of the tides, or during periods of minimal tidal movement. An additional

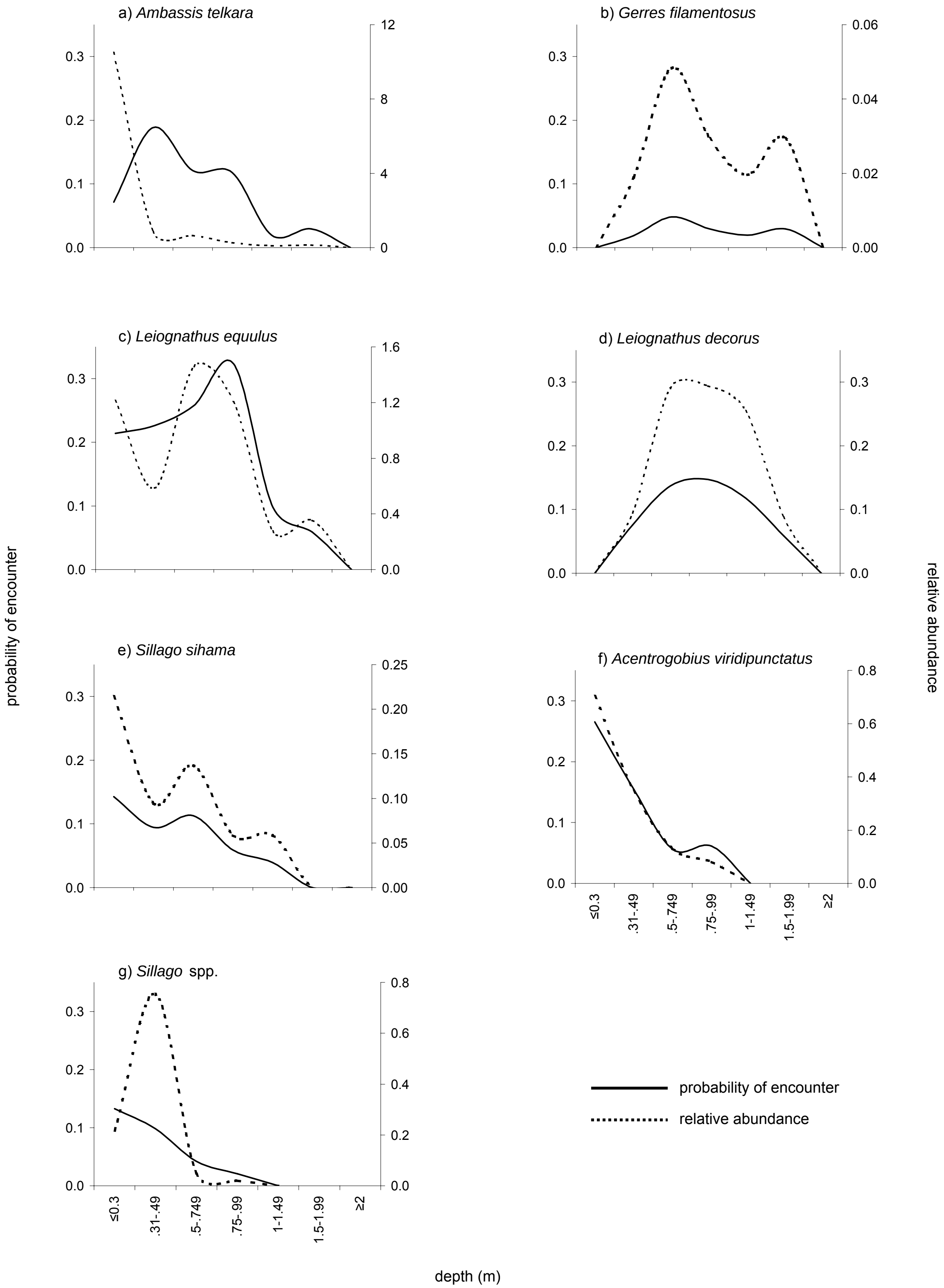


Fig. 6.2: Depth distribution of some common small (<100 mm) fishes sampled from the lower reaches of tropical estuaries in north-eastern Australi (R. Johnston unpubl. data). a) - e) 18 mm cast net (n = 388 nets), f) - g) 6 mm cast net (n = 950 nets). Note that for f) and g) sample sizes in >1.5 depth were insufficient for analysis (≤10 nets). Probability of encounter is the proportion of nets in which a taxa was present, relative abundance is the average number of individuals per net.

problem with longer soak times is the increased likelihood of predation by non-piscivores able to capture prey fatigued from being tethered for many hours.

Table 6.1: Size and identity of fish prey used in tethering experiments. (n) after the date indicates a night set.

Date	Species	# deployed	mean FL mm (± 1 SE)	# measured
24/07/03	*Leiognathus* spp.	6	45	1
22/08/03a	*Ambassis telkara*	11	51.5 (0.5)	11
22/08/03b	*Ambassis telkara*	11	52.1 (1.0)	9
12/09/03a	*Sillago* spp.	12	59.4 (2.0)	9
12/09/03b	*Sillago* spp.	12	61.2 (2.5)	11
12/11/03a	*Gerres filamentosus*	11	37.9 (0.5)	10
12/11/03b	*Sillago* spp.	9	59.1 (2.0)	9
10/12/03a	*Leiognathus* spp.	12	36.2 (1.7)	6
10/12/03b	*Sillago* spp.	12	65.2 (2.7)	9
5/01/04 (n)	*Leiognathus* spp.	10	48.0 (0.9)	7
6/01/04	*Sillago* spp.	11	68.1 (2.9)	7
29/01/04a	*Sillago burrus*	12	75.8 (1.4)	10
29/01/04b (n)	*Sillago* spp.	12	73.8 (1.3)	11
30/01/04a	*Sillago* spp.	12	52.6 (2.9)	9
30/01/04b	*Sillago* spp.	12	71.3 (2.2)	10
30/01/04c	*Sillago* spp.	9	46.7 (1.7)	9
30/01/04d (n)	*Liza vagiensis*	9	50.8 (1.7)	8

6.2.4 Analysis. The time and water depth was recorded at both deployment and retrieval of each chronograph. This was used in conjunction with measured survival time, observed tidal movements, and tide predictions from tide charts to estimate the depth at the time of predation. When no predation event was recorded, the median depth between deployment and retrieval was used in analyses.

Logistic regressions were used to test for a significant effect of depth on prey survival. If shallow waters provide the tethered fish with a refuge from predation, the data recorded as presence / absence (0 = survival, 1 = predation event), should show a sigmoidal response for both individual experiments and pooled across all experiments, providing a significant fit of a logistic regression (Fig. 6.3). The transition from survival to predation events would indicate a critical depth where predation pressure changes. Given the depth distributions of common small and juvenile fishes in this region (Fig. 6.2), such a transition would be expected at between 1-2 m depth. A lack of a significant fit of a logistic regression to the tethering data would indicate that predation pressure is not lower in shallow water than in the adjacent deep water.

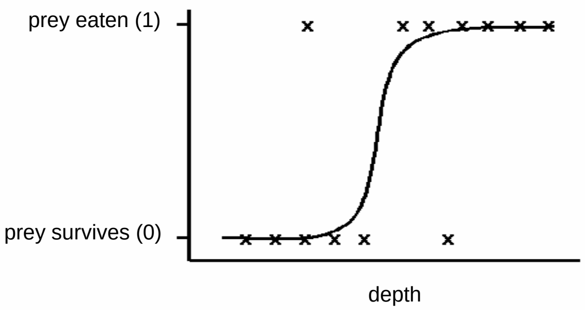


Figure 6.3: Hypothetical result of tethering experiments if shallow waters have lower levels of predation on tethered fish prey, and thus provide a refuge from predation. Result would be a sigmoidal response with a significant fit of a logistic regression.

6.3 RESULTS

6.3.1 General results. Seventeen trials were run for a total of 183 chronograph sets. Forty-six tethered fish (25%) were either missing (n = 32) or showed visible signs of attack by predators (n = 14) and these were recorded as predation events. A maximum of 7 predation events were recorded during a single trial, and during 2 trials no prey were taken or showed signs of attack. In one of the trials in which no prey were taken, all were retrieved dead and this trial was excluded from further analysis. Between one and three predation events were recorded during the three night trials.

Sampling was targeted at times of minimal water movement and the maximum change in depth recorded between deployment and retrieval was 0.7 m. Despite this and other efforts to ensure representative sampling across the depth range, the shallowest (<0.5 m) and deepest (>2.5 m) depth zones were underrepresented. Seventeen replicates were recorded in <0.5 m and 10 replicates in >2.5 m, while each of the 0.5 m depth zones between 0.5 and 2.5 m had between 34 and 41 replicate chronograph sets (Fig. 6.4). Note that the total of 174 sets excludes the trial when all nine tethered prey were retrieved dead.

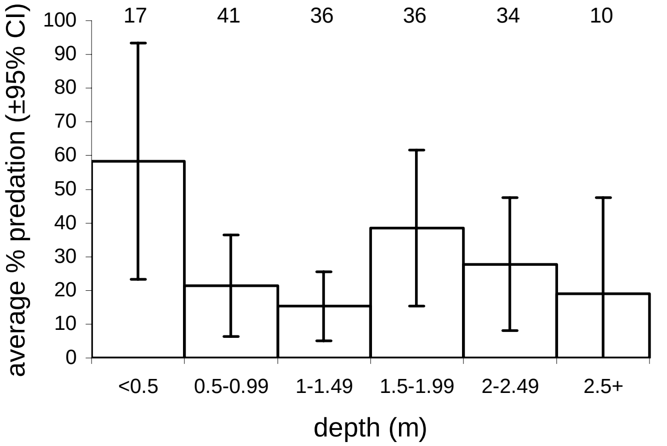


Figure 6.4: Profile of predation pressure on tethered fish across a depth gradient along sandy shores in the lower reaches of tropical estuaries, as measured by chronographic tethering experiments, n = 16 experiments. The total number of chronographs set in each depth zone is shown above each bar.

6.3.2 Patterns in predation pressure. Tethered prey were consumed across virtually the entire depth range sampled, with the shallowest and deepest predation events recorded in 0.15 m and 2.85 m respectively. Relative predation pressure was highly variable and no clear depth-related patterns emerged during the trials (Figs. 6.4 & 6.5).

Regardless of the level of pooling of the data, all logistic regressions were non-significant, thus providing no support for the shallow-water refuge hypothesis.

In four trials predation events were recorded only on individuals tethered in shallow waters (≤1.5 m), while in three trials predation pressure was focused on individuals tethered in deeper water (Appendix B). For the remaining trials in which predation events were recorded, prey were taken across the depth range or only at intermediate depths. Among the three night-time trials, one recorded predation events in shallow water, in one the only predation event was recorded in deep water and in the third, predation events were recorded across the depth range (Appendix B).

Averaged across all experiments, the highest average proportion (57 %) of tethered prey were consumed in <0.5 m of water (Fig. 6.4). However, sample size in this depth zone was low (n = 17), variability in predation pressure at all depths was high (Fig. 6.4), and the high average reflects a number of experimental trials in which each of the one or two prey tethered in <0.5 m were consumed. The profile of predation pressure was effectively the same whether viewed as the average percentage of tethered prey attacked per depth range per trial (Fig. 6.4), as the total proportion of individuals attacked per depth range pooled across all trials, or when only missing prey were counted as predation events. Including injured prey that were still attached to tethers as predation events had no effect on the profile of predation presented as the average proportion of individuals taken per depth range per trial (i.e. Fig. 6.4 has the same profile if injured prey were not counted), but it did slightly change the overall proportion of individuals taken per depth range. Overall there were proportionally more individuals injured but not taken in <0.5 m of water. The highest proportion of missing prey, pooled across all experiments, was between 1.5 and 2.5 m depth.

6.3.3 Survival time and chronograph success. The chronograph triggering mechanism worked reasonably well. Survival time was successfully measured for 25 of the 46 predation events (54.4 %). Twenty-three of the thirty-two predation events in which the tethered prey was missing successfully recorded survival time (71.9 %), while only 2 of the 14 events in which the prey was still attached to the tether but showed signs of attack successfully triggered the switch mechanism (14.3 %). Failure of the trigger mechanism when the prey was missing was usually due to sand fouling and jamming the switch slide, while failure of the trigger when the prey remained attached but showed signs of attack was apparently due to insufficient force on the tether line by predators. The switch was triggered 4 times (2.2 % of total sets) when the prey was not taken and showed no signs of attack by predators.

The average (± 1SE) survival time was 55 ± 8.7 minutes. Between one and eight successful measurements of survival time were recorded in each of the 0.5 m depth zones and there was no clear pattern in survival time related to depth (Fig. 6.5). The

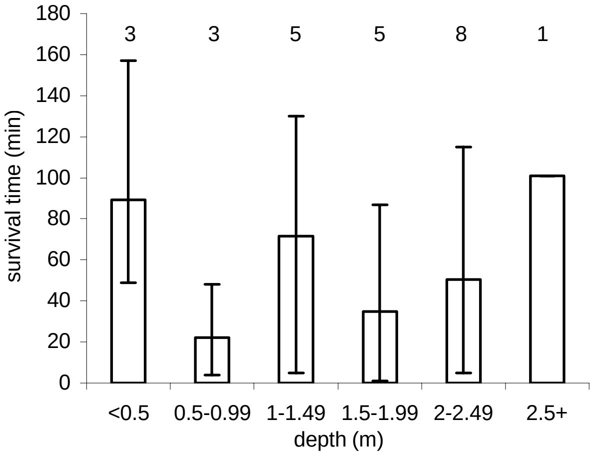


Figure 6.5: Average survival time of fish prey tethered across a depth gradient in the lower reaches of a tropical estuary, bars indicate range. The number of survival time records for each depth zone is shown above each bar.

shortest recorded survival time of 1 minute was recorded in 1.8 m of water, while the longest survival time measurement of 157 minutes was recorded at 0.35 m depth.

6.4 DISCUSSION

6.4.1 Experimental validity. Before interpretation and discussion of the measured depth-related patterns (or lack thereof) in predation pressure, it is important to first determine the validity of the experimental design in light of potential confounding factors. Efforts were made to overcome potential problems associated with the tethering technique reported in previous tethering studies. The most serious issue confronting the interpretation of tethering studies is the potential for interactions between artefacts of tethering and the treatment (Peterson & Black 1994). Such interactions may result in the measured patterns in predation potential bearing little resemblance to the natural patterns in predation pressure, making the results of tethering experiments meaningless. Interactions between tethering and treatment may result from differences in the behaviour or escape responses of tethered prey between habitats (treatments) (e.g. Barshaw & Able 1990, Curran & Able 1998). For example, the ability of tethered juvenile lobsters to burrow and escape predators differs to that of non-tethered lobsters in some habitats but not others (Barshaw & Able 1990).

Serious interactions between tethering artefacts and treatment are most likely to occur in studies comparing habitats that differ considerably in physical structure, where the treatments are widely separated, and/or the assemblages of potential predators are known to differ between treatments (Peterson & Black 1994), for example, comparisons between seagrass and non-vegetated habitats (e.g. Heck & Wilson 1987, Peterson et al. 2001). The assessment of potential interactions between tethering artefacts and treatment is very difficult (Peterson & Black 1994), however the potential for significant interactions in the present study was minimal. The treatment (depth) was a continuous variable, gradually changing across an experimental site with the deepest and shallowest treatments separated by <100 m of gradually sloping, basically featureless sandy bottom. Other than depth, all observable habitat characteristics which may interact with, and affect the vulnerability of tethered prey remained constant. It seems unlikely that the effect of the tether on prey behaviour and vulnerability would vary substantially across the depth range sampled.

The simple physical structure of the study sites used in the present study and the location of all depth treatments within a single site minimises the probability of significant differences in the suite of potential predators between treatments. A large proportion of the fishes capable of attacking or removing the prey tethered in this study are naturally piscivorous to some degree (Ch. 3 & 4), making them legitimate potential predators. Potential scavengers such as portunid crabs are relatively abundant in some estuarine habitats in the region (e.g. Haywood et al. 1998), however these rarely occur in seine net or trap samples from habitats such as those used in this study (Baker & Sheaves unpubl. data) and it seems unlikely that crabs would have contributed significantly to the measured predation events. Birds inflict heavy mortality on fishes occupying shallow estuarine habitats in some parts of the world (e.g. Whitfield & Blaber 1978a, Whoriskey

& Fitzgerald 1985, Deiperink 1994, Crowder et al. 1997) and prey tethered in shallow waters may become particularly vulnerable to avian predators. However, avian predation appears to be less important in tropical estuaries of north-eastern Australia (Blaber 1980) and there were no observations of actively feeding birds during the experimental trials. Thus the potential for any depth-related patterns in predation pressure to be confounded with predation by predators not normally capable of capturing non-tethered prey seems minimal in the present study.

The refuge paradigm has been broadly applied to all small fishes that utilise shallow-water tropical estuarine habitats (e.g. Blaber 1980). Surveys of the fish faunas of estuaries in north-eastern Australia consistently report well in excess of 100 species (Robertson & Duke 1987, Blaber et al. 1989, Haywood et al. 1998, Sheaves 2006), and sometimes more than 200 species (Blaber 2000). The piscivore assemblage of these systems is also highly diverse, not only in terms of species richness but in predation strategies, dietary habits and size structure (Ch. 3). Consequently, prey fish tethered in the habitats sampled during the present study were vulnerable to an unpredictable combination of members of a large and diverse piscivore assemblage.

Curran and Able (1998) found species-specific artefacts during laboratory studies comparing the effects of tethering on prey behaviour and vulnerability for different combinations of predators and prey. They concluded that experiments using tethered fish should be interpreted with caution and that laboratory experiments should be conducted to examine predator and prey species-specific artefacts before field trials are run (Curran

& Able 1998). While caution is clearly required in interpreting tethering studies, the extensive laboratory experiments required to adequately examine species-specific artefacts for different predators from such a diverse piscivore assemblage were well beyond the scope of the present study. For example, the aquarium facilities required to house and replicate experiments examining predation by piscivores ranging from small relatively sedentary predators such as small platycephalids, up to large highly mobile predators such as carangids, would be immense and were simply not available.

Because of the experimental design, the structure of the study sites and the efforts to overcome potential confounding problems, as discussed above, I believe the results of the present study are reliable and can be interpreted as reflecting natural depth-related patterns in predation pressure.

6.4.2 Depth-related patterns in predation pressure. Despite widely held views, and the findings of previous studies (e.g. McIvor & Odum 1988, Ruiz et al. 1993, Manderson et al. 2004), there was no clear evidence that predation pressure on small juvenile fishes was lower in shallow waters than in the adjacent deeper waters in the present study. The profile of predation pressure was highly variable. In some experimental trials, predation was focussed in deeper waters (>1.5 m), while in others predation events were recorded exclusively on fish tethered in shallow water. Tethering studies from other parts of the world have detected clear differences in predation pressure between treatments (Table 6.2). While not all of the studies listed in table 6.2 examined the effect of depth on predation pressure, the sample sizes were large enough in each study to detect a clear

Table 6.2: Summary of experiments tethering mobile nekton in estuarine habitats. ? insufficient information; * missing prey replaced during experiment; - did not use chronographs.

Location	prey	trials (total sets)	soak time (h)	mortality (%)	av. Survival time (min)	distance between tethers (m)	chronograph efficiency (% successful record)	source
northern Australia	fish (various spp.)	17 (183)	2-3	25.1	55	≥20	54.4	this tudy
northern Australia	shrimp (*Penaeus* sp.)	3 (92)	12	53.1 - 92.9	294 - 583	<3	73.5	Haywood & Pendrey (1996)
Rhode Island USA	fish (*Fundulus heteroclitus*)	9 (270?)	120-192	?*	-	?	-	Halpin (2000)
New Jersey USA	fish (*Pseudopleuronectes americanus*)	12 (239)	4	54	96	3	24	Manderson et al. (2004)
Virginia USA	fish (*Fundulus heteroclitus*)	4 (80)	2-3	10-30	-	≥2	-	Rozas & Odum (1988)
Chesapeake Bay USA	fish (*Fundulus heteroclitus*)	1? (68)	1.5	46	-	2	-	Ruiz et al. (1993)
Chesapeake Bay USA	fish (*Fundulus heteroclitus*)	3 (90)	2-3	17.8	-	?	-	McIvor & Odum (1988)
Chesapeake Bay USA	shrimp (*Palaemontes pugio*)	12 (216-288?)	2.5	<20 - >60	-	?	-	Clark et al. (2003)
Maine & Florida USA	shrimp & crab	13 (222)	12	30.2*	15 - 315	≥3	61.2	Peterson et al. (2001)
Texas USA	shrimp (*Penaeus aztecus*)	1 (39)	≥19	95	266 - 711	mean = 100	33.3-66.7	Minello (1993)

pattern between treatments. For example, in just three experimental trials McIvor & Odum (1988) found a clear and consistent pattern of higher predation pressure on fish tethered in deep waters adjacent to erosional banks than on those tethered in shallower water on depositional banks. The lack of any clear depth-related pattern in predation pressure in the present study was despite a sample size similar to or greater than many previous studies (Table 6.2).

The findings of this study suggest that the shallow-water refuge paradigm may be too simplistic for dynamic and species rich tropical estuarine nursery grounds. The studies which have provided the strongest direct support for the shallow-water refuge paradigm have all been from temperate systems in North America (McIvor & Odum 1988, Ruiz et al. 1993, Clark et al. 2003, Manderson et al. 2004), which have much less diverse piscivore assemblages than estuarine systems of the tropical Indo-West Pacific (Hartman & Brandt 1995, cf. Baker & Sheaves 2005). Given the diversity and complexity of the piscivore assemblage in this region, the suite of piscivores present and the level of predation pressure within estuarine habitats is likely to show considerable spatial and temporal variability. When this complexity is considered, it is hardly surprising that no clear depth related pattern in predation pressure was apparent. While a larger sample size may have revealed a clearer depth-related pattern in predation pressure, it seems likely that the variability in predation pressure measured during this study is reflective of a highly diverse system in which any depth-related patterns in predation pressure are complex and difficult to predict.

6.4.3 Implications for refuge paradigm and nursery ground functioning. Predation has the potential to be a major structuring force on shallow water estuarine nursery assemblages, particularly through the consumption of new recruits (Scharf et al. 1998b, Sheaves 2001, Ch. 3 & 4). Prey smaller than those used in the present study could not be successfully tethered due to high mortality during capture, handling and tethering. Consequently, the prey used during the present study (Table 6.1) were quite large relative to their size at recruitment (Robertson & Duke 1990b, Chapter 4 this study) and relative to the size of many of the piscivores found in shallow tropical estuarine nurseries (Ch. 3 & 4). Thus the measured predation pressure is unlikely to represent predation pressure on new recruits because the tethered prey were not vulnerable to the same range of predators as new recruits. However, if there is no clear shallow-water refuge for fish of the size tethered, then it is unlikely there would be a refuge for smaller fish. This is because the shallow-water refuge paradigm implies that small fish gain access to water that is shallow enough to exclude larger fish which prey on them (Ruiz et al. 1993). For example, if 1 m deep water does not exclude the predators of *Sillago* spp. 45 - 75 mm tethered during this study, then it seems unlikely that it would provide refuge for *Sillago* recruits <20 mm. The results from the present study indicate that juvenile fishes inhabiting shallow water habitats in estuaries in this region do not gain any clear benefit of reduced predation pressure relative to adjacent deeper waters, in contrast to the results from temperate North America. Due to the diversity of these tropical systems, the processes structuring juvenile fish distribution are likely to interact in complex ways and the shallow water refuge paradigm appears too simplistic for application to tropical estuarine nurseries.

Chapter 7

Predation on new recruits: the relative impact of different piscivores in shallow estuarine nurseries.

ABSTRACT

A model was developed to estimate the relative impacts of different functional groups of piscivores on the shallow-water estuarine nursery assemblage. 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 piscivores, have the potential to have orders of magnitude greater impacts than more conspicuous larger piscivores on new recruits utilising shallow tropical estuarine habitats as nurseries. Because of their sheer abundance, a switch by the minor piscivores to target new recruits results in a massive increase in the consumption of fish prey by the piscivore assemblage. As a broad functional group, minor piscivores occur in many systems around the globe, and are likely to play important roles in these systems as predators that shape communities by targeting the critical early life stages of other fishes.

7.1 INTRODUCTION

Shallow tropical estuarine nurseries contain a diverse assemblage of piscivores, ranging from tiny new recruits, up to large mobile predators that may periodically enter shallow estuarine habitats to feed (Ch. 3-5). The larger, more conspicuous or ‘obvious’ predatory taxa such as carangids, platycephalids and sphyraenids, are widely recognised as important piscivores within tropical estuarine systems (Blaber 1986, Salini et al. 1990, 1998, Haywood et al. 1998). Fish dominate the diets of these predators (Salini et al. 1990, Ch. 3 this study) and larger individuals of some species regularly consume fish prey in large numbers (Ch. 3). Consequently there appears to be a general impression that the large primary piscivores are the only predators of significance in structuring estuarine fish assemblages and the functioning of nurseries (see review by Sheaves 2001).

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. However, many members of the lower trophic groups also include small quantities of fish in their diets (Salini et al. 1990, Haywood et al. 1998, Ch. 4 this study). These occasional or 'minor' piscivores (Whitfield & Blaber 1978a) appear to switch to target fish prey in response to recruitment events of small fish into the estuarine nurseries (Martin & Blaber 1983, Ch. 4 this study). Typically, minor piscivores numerically dominate samples from shallow estuarine habitats (e.g. Robertson & Duke 1987, Blaber et al. 1989, Sheaves 2006), and thus have the potential to contribute significantly to the predation pressure on new recruits entering the shallow-water nursery (Ch. 4 this study).

Clarifying the relative importance of different types of predators is central to gaining a clearer understanding of predation dynamics and shallow nursery ground function. One of the greatest challenges to achieving this is quantifying the relative abundance of different members of diverse predator assemblages such as those of tropical estuaries (Ch. 3). Gears such as seine nets, that provide quantitative abundance estimates of small and juvenile fishes in shallow water habitats, are not efficient in capturing larger or more mobile individuals (Kneib 1997, Rozas & Minello 1997, Ch. 5 this study). Similarly, while gill nets can be effective at capturing large numbers of mobile fishes such as carangids (e.g. Blaber et al. 1989), they are size selective, and passive (relying on fish to move into them for capture). These features of their mode of operation mean that abundance estimates derived from gill nets (CPUE) are not comparable to those derived from other gears (Smith & Hindell 2005). One useful approach to quantitatively sample an entire fish assemblage is block netting, whereby a large area of habitat is fenced off, and all fish above net selection size are captured (e.g. Davis 1988, Paterson & Whitfield 1996, Barletta et al. 2003). However, this technique is limited in the locations or habitat types in which it can be effectively employed, and thus is likely to provide a snapshot of only a subset of the entire shallow water estuarine fish fauna.

The aim of this chapter is to estimate the relative magnitude of potential predation mortality inflicted by different members in the piscivore assemblage on juvenile fishes using shallow estuarine nurseries. This was achieved by bringing together data on the variability in occurrence of fish in the diet of various piscivores (Chapters 3 & 4), and combining this with data on the composition and abundance of a shallow-water intertidal estuarine fish assemblage gained by block netting. From this, a model was produced that estimates the relative predation impacts of different groups within a real estuarine fish assemblage.

7.2 METHODS

7.2.1 Piscivore relative importance model (PRIM). To estimate the relative impacts of each piscivore taxon/size class, the PRIM multiplies the proportion of individuals likely to consume fish prey (% frequency of occurrence) by the abundance of that taxon/size class. 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 taxon/size class.

The PRIM could be used to model a range of scenarios and/or to examine the impacts of the piscivore assemblage at a range of levels or scales (e.g. comparisons between groups of species, between individual species, or between size classes within a species). For the purpose of this study, the model was used to examine the magnitude of the potential impacts of major and minor piscivores on shallow water nursery assemblages during and between recruitment events using the abundance data from block net sampling (see 'Model scenarios' below). The model estimates the relative impacts of individual size classes or taxa under each of the scenarios and provides a summary of the pooled relative impact of major and minor piscivores.

The potential impacts of three groups of piscivores, *Ambassis 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 also examined. 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 (see 'Predicting predation impact of other estuarine piscivores' below).

While obviously relevant to many trophic studies, biomass values were not used in the model. Only abundance values were used. The goals of this study were to examine the potential levels of predation mortality on prey fish populations, not aspects of energy flow through the food web. Consequently, abundance values were considered more appropriate. However, prediction of predation impacts on new recruits by various members of the piscivore assemblage, based on predicted numbers of new recruits consumed, would roughly approximate the relative biomasses consumed because in this scenario all prey are approximately the same size (all new recruits 10 - 20 mm).

7.2.2 Construction of the PRIM. Each taxon was divided into size classes that reflect 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 of piscivory and maximum size of consumption of new recruits. As such, each size class can be considered a functional group. For example, while the flathead *Platycephalus fuscus* may generally be considered piscivores (Ch. 3, Table 3.1), each of the size classes used is functionally different in terms of the predation pressure exerted on the prey fish assemblage; new recruits <20 mm were not found to eat fish, small individuals (<50 mm) occasionally consumed 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 (Ch. 3, Fig.

3.5, 3.6). Details of the statistical techniques used to identify functional groups are presented in appendix C.

For each functional group, data were summarised on the frequency of occurrence of fish, total number of fish prey (hereafter abbreviated to ‘total fish’) and number of non-pelagic or demersal new recruits (‘new recruits’). Demersal new recruits are defined as small new recruits (≤20 mm) with some direct trophic links to, and/or use of, the shallow water nursery. Clupeoids, hemirhamphids and atherinids were not included in calculations of the numbers of new recruits consumed by predators. These groups do not show the same strength of preference for shallow water habitats exhibited by many of the small and juvenile fishes in these systems (Johnston unpubl. data) and feed primarily in planktonic/pelagic food chains. 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. (However, the presence of high densities of pelagic prey (e.g. clupeoids) may influence predation pressure by certain predators on demersal fishes within shallow nurseries - see Implications and Conclusions, Ch. 3).

7.2.3 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 7.1).

Table 7.1: 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 D.

	minor		major	
Scenario	% 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)

The ‘no switching’ scenario assumes none of the piscivores specifically switch to target new recruits and that 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 (Ch. 4) and incorporate information on the variability in the consumption of fish prey.

Because, by definition, major piscivores prey primarily on fish (Whitfield & Blaber 1978a), the average occurrence and average number of total fish prey should represent their consumption of fish between recruitment events, and these values were used for the ‘between recruitment’ scenario (Table 7.1). Furthermore, the frequency of occurrence of fish in the diet of major piscivores can not increase much 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 7.1).

In contrast to the overall high level of consumption of fish by major piscivores, minor piscivores usually feed on alternate prey, while occasionally switching to prey heavily on new recruits (e.g. Martin & Blaber 1983, Ch. 4 this study). As a consequence of the highly skewed spatio-temporal distribution of the consumption of fish prey (Fig. 4.2), 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)(Ch. 4). Therefore, to model the predation impact of minor piscivores, the modal frequency of occurrence (which is <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 7.1).

The model scenarios essentially cover the spectrum of potential impacts of each type of predator on prey populations, allowing assessment of the robustness of the conclusions drawn from the model. If the same conclusions are drawn from the two extreme scenarios, for example that a functional group has the potential to exert considerable predation mortality on prey fish populations under the conservative 'between recruitment' scenario, then a conclusion that these predators are important in the shallow nursery can be made with confidence. Conversely, if a predator was predicted to only contribute significant mortality under one scenario (i.e. high occurrence and numbers of prey under the 'during recruitment' scenario) then conclusions as to the importance of such a predator would need to be more cautious.

7.2.4 Derivation of model parameters. Average frequency of occurrence values were derived from smoothed ontogeny models (e.g. Fig. 3.5, Ch. 3), or directly from the gut content summaries in chapter 3. Published dietary data for six species (*Ambassis telkara* [Haywood et al. 1998, Davis 2001], *Sillago maculata* [Maclean 1971], *S. sihama* [Gunn & 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 & Blaber 1978b]), was in sufficient detail to allow the combination of the published data with that from this 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 occurrence in individual net shots or sampling occasions (e.g. Table 4.2, Chapter 4), or from published literature (*A. telkara* – Davis 2001, *S. sihama* – Gunn & Milward 1985, *S. barracuda* – Blaber 1982). Average and maximum numbers of total fish prey and new recruits were derived from quantile regressions of the predator size – number of prey relationships (e.g. Fig. 3.6, Ch. 3) or taken directly from the raw gut content data. When the frequency of occurrence and number of fish prey values were based on the smoothed ontogeny models or quantile regressions, the values used for each size class were the predicted values for the size class midpoint.

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

Abundance data was collected by block net sampling a high intertidal marsh in Blacksoil Creek (19^o 18' S, 147^o 3' E, Fig 3.1) to provide absolute abundances to use in the piscivore relative importance model. Using block netting, any fish too large to pass through the net mesh is retained with equal efficiency, regardless of size, mobility or behaviour (Paterson & Whitfield 1996). Consequently, the technique ensured, as far as is practically possible, that all fish (unable to pass through the 12 mm mesh block net) on the marsh surface at high tide were captured and counted, thereby providing a complete snapshot of the composition, abundance and biomass of an entire fish assemblage.

The study site was in the lower reach of the Blacksoil Creek estuary, <1 km upstream from the mouth (Fig. 7.1). On a 2.7 m high tide, there is approximately 1 ha of flooded

Figure 7.1: Block net site on Blacksoil Creek marsh. Dotted line shows approximate water level on 2.7 m high tide. Solid line indicates block net position across the 30 m wide entrance channel.

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 would 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 hrs 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 was 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 x 2 m, 12 mm knotless mesh) was set by hand at slack high water across the entrance of the marsh. PVC poles were used to hang the net. The lead line was attached to the poles with wire hooks and driven ~10cm below the sediment surface. Between the poles the lead line was buried in a pre-dug trench to prevent fish escaping under the net. The float line was suspended ~50 cm above the waters surface (at high tide) from hooks on the poles to prevent fish from jumping 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 (into 10 mm size classes) weighed (in size classes), 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).

7.2.6 Predicting predation impact of other estuarine piscivores. The potential impacts of three groups of piscivores, *Ambassis 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.

(i) *Ambassis 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 7.1).

(ii) Large carangids. *Caranx sexfasciatus* >148 mm consumed the greatest average and maximum number of demersal new recruits of all the predators examined in this study (appendix D). 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 "during recruitment" scenario using both the average and maximum number of new recruits per *C. sexfasciatus* (Table 7.1, 3a & b).

(iii) *Platycephalus* spp. As for *C. sexfasciatus*, the numbers of medium to large flathead 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.

7.3 RESULTS

7.3.1 Potential responses of different piscivore groups to recruitment events. Among the fishes examined for dietary analysis during this study (Table 3.1), 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 7.2). The minor piscivores show a greater difference between average and maximum frequency of occurrence of fish (Table 7.2); on average few individuals consume fish prey, but occasionally a large proportion will do so.

Table 7.2: Responses of piscivores to changes in the availability of fish prey, based on the gut contents of 4985 fishes from more than 50 taxa (Ch 3). Parameter values are averaged (± 1 SE) across all taxa/size classes within the functional group. Parameter values for individual taxa/size classes are presented in appendix D. *data for *M. cordyla* (n=1) excluded from calculations.

	parameter					
	% freq. occurrence		# total fish		# new recruits	
piscivore functional group	av.	max.	av.	max.	av.	max.
minor	17.2 ± 2.2	59.3 ± 5.1	1.5 ± 0.2	3.0 ± 0.6	1.6 ± 0.2	2.0 ± 0.4
major excluding carangids	76.9 ± 3.4	93.9 ± 2.2	1.9 ± 0.2	5.6 ± 1.1	1.4 ± 0.2	2.3 ± 0.3
carangid major piscivores*	82.7 ± 3.8	96.3 ± 2.6	15.7 ± 6.1	48.3 ± 17.0	7.9 ± 2.4	14.5 ± 4.0

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 7.2). 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 little difference between the average number of total fish prey and the average and maximum number of new recruits. This indicates that in general these groups do not respond to recruitment events by increasing the number of fish prey consumed per individual. On average, minor piscivores consume more new recruits than the major piscivores excluding carangids (Table 7.2).

Individual carangids consume more new recruits than the other piscivores (Table 7.2). However, the carangids have a lower maximum number of new recruits than the average number of total fish, indicating that overall the carangids also do not respond to recruitment events by switching to consume large numbers of new recruits (Table 7.2). The number of fish prey consumed by the carangids is quite variable (Table 7.2), and among the individual taxa/size classes of carangids there are a variety of responses. Several of the carangids consume few demersal new recruits compared to the average and maximum total fish prey, e.g. *Atule mate, Caranx ignobilis* >117 mm, *Scomberoides commersonianus* ≥60 mm, *S. tala* (Appendix D). Conversely, some carangids consume large numbers of fish prey including large numbers of new recruits, e.g. *Caranx sexfasciatus* and *S. lysan* >140 mm. Although individual piscivore taxa/size classes can respond differently to changes in the availability of fish prey, 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 7.2).

7.3.2 Predation on the Blacksoil Creek marsh. A total of 19 842 fish (including sharks & rays) 1 squid and 8 mud crabs (*Scylla serrata*) were collected in the 6 Blacksoil marsh samples (see appendix E for total catch composition). 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. 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, being mainly atherinids, clupeids, gerreids and leiognathids. Consequently, the model potentially underestimates significantly 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 7.1), 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 7.3). 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.

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 7.3). 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,

Table 7.3: 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

	scenario											
	between recruitment events				**no switching**				**during recruitment events**			
	number of prey			%	number of prey			%	number of prey			%
date	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**

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.

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 7.3). The Nov 03 sample of piscivores had the highest predicted impact on new recruits on the Blacksoil marsh, and minor piscivores accounted for 96.9 % of this predicted impact. When the major piscivore impact was estimated using the maximum occurrence and maximum number of new recruits per individual (Table 7.1; 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.

7.3.3 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 7.4). In fact, under each scenario it was a minor 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; *S. lysan* 20-54 mm (1st), *Sillago analis* (4th) and *S. 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* *stronglylura* (ranked 3rd) and *Tylosurus crocodilus* (7th), the sphyraenid *Sphyraena barracuda* (5th), the platycephalids *Platycephalus fuscus* (6th) and *P. endrachtensis* (10th), and the plueronectid *Pseudorhombus arsius* >30 mm (9th).

Under the no switching scenario, the minor piscivores *Scomberoides lysan* <55 mm and *Sillago ciliata* rank 1st and 2nd respectively among all the piscivore groups (Table 7.4). Five of the top ten highest ranked piscivore groups were minor piscivores under this scenario, and included *Sillago analis* (4th), *Ambassis telkara* (6th) and *Terapon jarbua* (7th). The model predicts that during recruitment events minor piscivores rank eight of the top ten highest impacts on new recruits (Table 7.4). *S. lysan* ≥55 mm and *S. 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 (*Sphyraena barracuda, Platycephalus 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 7.4). This is because certain sized individuals in these groups consume few or no new recruits (e.g. *P. fuscus* >300 mm, Ch. 3). 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.

Table 7.4: Relative importance of different piscivore functional groups on the Blacksoil marsh, pooled across all samples. Bold: minor piscivore.

	scenario					
	between recruitment		**no switching**		**during recruitment**	
piscivore functional group	rank	total fish	rank	total fish	rank	total fish
Scomberoides lysan **20-54mm**	**1**	**121.7**	**1**	**180.1**	**4**	**269.0**
S. lysan ≥55mm	2	101.4	3	101.4	7	189.7
Strongylura strongylura ≥40mm	3	63.8	5	63.8	8	93.6
Sillago analis **≥30mm**	**4**	**32.3**	**4**	**71.0**	**1**	**1936.2**
Sphyraena barracuda ≥20mm	5	19.2	8	19.2	16	8.0
Platycephalus fuscus ≥50mm	6	16.8	9	16.8	23	1.1
Tylosurus crocodilus ≥40mm	7	14.8	10	14.8	13	18.0
Sillago ciliata **≥30mm**	**8**	**13.0**	**2**	**116.6**	**2**	**666.0**
Pseudorhombus arsius >30mm	9	11.5	11	11.5	14	11.5
Platycephalus endrachtensis ≥50mm	10	10.9	12	10.9	15	9.8
Tylosurus gavialoides ≥40mm	11	10.2	14	10.2	17	6.5
Ambassis telkara **>20mm**	**12**	**7.6**	**6**	**40.2**	**3**	**503.7**
Gerres filamentosus **>20mm**	**13**	**7.3**	**15**	**7.3**	**5**	**266.8**
Terapon jarbua **≥30mm**	**14**	**2.4**	**7**	**21.7**	**6**	**253.4**
Sillago sihama **≥30mm**	**15**	**2.4**	**17**	**5.9**	**11**	**28.4**
Psammogobius biocellatus	16	1.9	20	1.9	19	2.8
Lutjanus fulviflamma **≥20mm**	**17**	**1.8**	**19**	**2.3**	**20**	**2.3**
Stolephorus sp. ≥40mm	18	0.9	13	10.3	12	18.8
Acanthopagrus berda **>20mm**	**19**	**0.6**	**16**	**6.3**	**10**	**34.3**
A. australis **>20mm**	**20**	**0.5**	**18**	**5.0**	**9**	**46.5**
Scomberoides commersonianus **20-59mm**	**21**	**0.3**	**21**	**0.9**	**21**	**1.5**
P. fuscus **20-49mm**	**22**	**0.1**	**22**	**0.2**	**22**	**1.1**
Sillago maculata **≥30mm**	**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

7.3.4 Predicting predation impact of other estuarine piscivores. Sixty-seven *Ambassis telkara* (<0.007 ind. m^{-2}) could potentially inflict greater predation pressure on new recruits on the Blacksoil marsh than did the 56 major piscivores sampled in April 2003 (Table 7.5). This was the sample with the highest predicted predation pressure by major piscivores under the 'during recruitment' scenario (Table 7.3). In fact, 213 individuals (0.021 ind. m^{-2}) could consume more new recruits than the predicted total consumption by major piscivores pooled across all six sampling occasions (Table 7.5).

Even if the maximum proportion of major piscivores were to consume the maximum number of new recruits recorded per individual (Table 7.1, scenario 3b), 177 *A. telkara* (0.018 ind. m^{-2}) modelled under the 'during recruitment' scenario would exceed the impact of the major piscivores sampled in April 2003, while 529 individuals (0.053 ind. m^{-2}) would consume more than all the major piscivores combined.

Table 7.5: 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 7.1. 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	67	0.0067
	major piscivores, pooled all samples, scenario 3a	340.9	213	0.0212
	all piscivores November 03	1134.5	707	0.0706
	major piscivores, April 03, scenario 3b	284	177	0.0177
	major piscivores, pooled all samples, scenario 3b	848.4	529	0.0528
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
Platycephalus fuscus 80-300 mm				
scenario 3a	minor piscivores April 03	286.8	216	0.0216
	minor piscivores November 03	1328.1	999	0.1000
scenario 3b	minor piscivores April 03	286.8	76	0.0075
	minor piscivores November 03	1328.1	350	0.0350

Seven-hundred and seven *A. telkara* (0.071 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 7.5), the occasion with the greatest predicted total impact on new recruits (Table 7.3).

Eleven *Caranx 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 7.5). When the impact of *C. sexfasciatus* was predicted under the 'during recruitment' scenario (b), the required abundances were 7 and 29 respectively. Similarly, 216 and 999 *Platycephalus 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 7.5). If the maximum proportion of flathead were consuming the maximum recorded number of new recruits per individual (during recruitment scenario b), then 76 and 350 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.

7.4 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 & Blaber 1978a, Blaber 1980, Blaber 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.

7.4.1 Model assumptions and interpretation. Ontogenetic dietary changes for many of the piscivore taxa are gradual (e.g. Fig. 3.5) and likely to be spatio-temporally variable. As such, the size classes used in the model 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. For example, it is assumed that the average of 1 fish in each *Sillago analis* and 10 in each medium sized *Caranx sexfasciatus* means *C. sexfasciatus* actually eats 10 times the number of fish in the same time period, and not that the *Sillago* eats the same amount but digests it more quickly.

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 hours to completely digest the prey (Baker unpublished data, appendix F). Similar experiments indicate that the clupeid *Herklotsichthys* sp. digests planktonic crustaceans (*Artemia*) in 6 hours (Knott 2005). The rate of prey digestion is largely controlled by temperature (Fange & Grove 1979, Weatherley & Gill 1987), and is thus likely to be relatively constant across predatory fish taxa within any particular environment.

Given the results of the digestion rate experiments, the gut contents of any predator examined during this study was assumed to represent approximately the last 6 hours of feeding. To make an estimate of the total number of fish prey consumed by each group per day, the values from the model could simply be multiplied by 2 for species that fed during daylight hours only, or by 4 for any species that feeds continuously day and night. There is no published data on diel feeding patterns for the predator species examined in this study, and due to the logistical difficulties of sampling, no samples were collected at night to examine gut contents. Examination of gut content data for individuals collected throughout the day and across a range of tidal cycles gave no indication of any diel or tide-related feeding periodicity among the species examined (Baker unpublished data). A large proportion of the individuals examined for gut contents during this study were below 100 mm FL (Table 3.1), and it appears these small individuals will feed whenever the opportunity exists. Larger individuals were not captured in sufficient numbers at any location or time to examine such patterns.

7.4.2 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 occurs 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 7.2). 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 7.3), primarily as a function of the increase in the frequency of occurrence of fish in the diet of these highly abundant predators (Table 7.2). In contrast, the relatively small changes in the frequency of occurrence of fish prey among the low abundance major piscivores has little effect on the overall predation impact of these predators (Table 7.2, 7.3).

Major piscivores prey primarily on fish (Whitfield & Blaber 1978a). Many of those examined during this study include demersal new recruits in their diet (Table 7.2, appendix D), 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). The predator-prey size relationships indicate that ambush predators such as *Platycephalus* spp. and *Pseudorhombus arsius* generally consume relatively large fish prey (Fig. 3.6, Ch. 3). 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 (Fig. 3.6, Ch. 3). While *Caranx sexfasciatus* and *Scomberoides 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 & Shaw (1995b) found a similar division in prey types consumed by piscivorous fishes in a southern Australian estuary, with the benthic 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 7.2, Appendix D). 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.

7.4.3 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 7.3). It is clear then, that regardless of whether the evidence for prey switching presented in chapter 4 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 (Blaber 1980, Robertson & Duke 1987, Blaber et al. 1989, Blaber & 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 *Ambassis telkara, Acanthopagrus berda, Sphyraena barracuda* and *Terapon jarbua* extend well into subtropical systems in both Australia and southern Africa (e.g. Whitfield & 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. For example, *Ambassis marianus, Acanthopagrus australis* and *Sillago analis* all were far more abundant than any of the primarily piscivorous taxa sampled from mangrove forests in subtropical Moreton Bay, Australia (Morton 1990).

7.4.4 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 called *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 & Blaber 1983, Blaber et al. 1985, 1989, Robertson & Duke 1990a, b, Sheaves 2006). *A. telkara* shows a strong affinity for shallow-water habitats (Johnston unpubl. data; Fig. 6.2) and may switch from zooplankton to prey heavily on fish recruiting to estuarine nurseries (Martin & Blaber 1983, Ch. 4 this study).

Sheaves (2006) recorded *A. telkara* in shallow sandy habitats in the lower reaches of nine local estuaries (including Blacksoil Creek) at average (± 1 SE) densities of 0.20 ± 0.05 individuals 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 (~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 – 0.071 ind. m^{-2}, Table 7.5) 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. In fact, large schools of *A. telkara* could exert massive mortality on new recruits entering the estuary on a single incoming tide, 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 *Caranx sexfasciatus* required to exceed the impact of the minor piscivores on the Blacksoil marsh may initially seem relatively low (Table 7.5). However, to place these figures into context it should be remembered that the predicted numbers of new recruits consumed per functional group represent the estimated consumption in approximately 6 hours of feeding (see model assumptions and interpretation above). Many of the minor piscivores dominate the shallow-water nursery assemblage (Robertson & Duke 1987, 1990, Sheaves 2006), and remain in shallow-water habitats most of the time (R Johnston unpublished data). 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, Ch. 5 this study). 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 6 hours (or for equal time as the 'resident' minor piscivores).

If a group of carangids were to enter the Blacksoil marsh to feed for, say, 10 minutes 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 a full 6 hours. It would take more than 1000 carangids feeding for 10 minutes to match the maximum predicted impact of minor piscivores on the Blacksoil marsh over one high tide. While the timeframe of ten minutes feeding over a six hour period is somewhat arbitrary in the absence of quantitative data on the periodicity of feeding by mobile piscivores in shallow waters (Ch. 5), it provides a prediction that can be tested against field observations. Qualitatively at least, observations suggest that these mobile piscivores probably do not enter shallow water habitats often enough or in large enough numbers to inflict the same amount of predation pressure on new recruits as the 'resident' minor piscivores (Baker pers. obs.).

Large flathead (*Platycephalus* spp. ≥100 mm) have been observed in shallow sandy habitats in this region at average densities of 0.043 individuals m^{-2}, and up to 0.197 m^{-2} (Ch. 5). These densities are equivalent to the predicted required density for flathead to match the impact of minor piscivores on the Blacksoil marsh (Table 7.5). However, the flathead observed during the visual surveys tended to form high density aggregations. It is not clear if the high observed 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 (Fig. 7.1). 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 (Ch. 5) potentially exert a significant proportion of the predation pressure on small fishes utilising these habitats. It should be remembered, however, that large flathead (*P. fuscus* > 300 mm) were not found to consume new recruits (Ch. 3). Individuals >300 mm accounted for almost 40 % of the flathead observed during the visual surveys (Ch. 5). 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.

7.4.5 Implications for the levels of predation in shallow estuarine nurseries. The details of the model parameters and outputs of the model depend on factors such as sample size of fishes collected for dietary analysis, and the spatio-temporal distribution of those samples, and as such should be interpreted as an approximate indication of the predation potential of different piscivore groups, rather than as precise values. It is clear however that the overall conclusions from the model are robust; that a range of predatory fishes that generally prey little on other fish are potentially the most important piscivores in shallow water nurseries.

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 (appendix E) 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 & Duke (1990a) 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 & 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 & Duke 1987, Blaber et al. 1989, Blaber & Milton 1990, Sheaves 2006), also dominated the assemblage sampled in the present study (Appendix E).

Robertson & Duke (1987) and Sheaves (2006) noted the replacement of particular species by congeners in different estuaries. For example, *Sillago 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 (appendix E). *S. 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 D). As such it would potentially be a major predator in other shallow estuarine habitats in the region, just as *S. analis* and *S. cilata* 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.

Obviously 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. There were almost 3500 potential piscivores sampled on the Blacksoil marsh that could contribute to the predation pressure on new recruits utilising these sorts of habitats. These were not included in the model due to insufficient dietary data. With the exception of just three individuals (1 *Elops hawaiiensis,* 1 *Negaprion acutidens* and 1 squid), all would be considered minor piscivores. The excluded minor piscivores are common components of tropical Indo-Pacific estuarine fauna, being mainly atherinids, clupeids, *Gerres* spp. and leiognathids (Blaber 1980, Robertson & Duke 1987, Blaber et al. 1989, Blaber & 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.

At a functional level, the Blacksoil marsh sample generally reflects the shallow water estuarine fauna from this region (Appendix E, Robertson & Duke 1987, Blaber et al.

1989, Milton & Blaber 1990, Sheaves 2006). The model predicts that minor piscivores are the most important among the piscivores sampled, and the minor piscivores excluded from the model are common throughout the region. Thus it seems reasonable to conclude that minor piscivores would exert the vast majority of predation pressure on new recruits in shallow-water estuarine habitats throughout the region.

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 & Cattrijsse 2004, Pasquaud et al. 2004; *Clupea harengus*, Maes et al. 2003), southern Africa (Martin & Blaber 1983), North America (e.g. White perch *Morone americana*, Monteleone & Houde 1992), the Bahamas (Layman & Silliman 2002), and temperate Australia (Edgar & Shaw 1995a, b). The low average occurrences of fish in the diets of these types of predators quite possibly reflects a switch to target periodically available new recruits (Martin & Blaber 1983, Monteleone & Houde 1992). 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 been missed

(Steele et al. 1998). Some of the piscivores that were not very important on the Blacksoil marsh (e.g. larger carangids) 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 (Kneib 1997, Rozas & Minello 1997, Smith & Hindell 2005). 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.

Predation on early life stages can play a major role in cohort survivorship and in structuring fish assemblages in other systems such as coral reefs (e.g. Carr & Hixon 1995, Hixon & Carr 1997, Webster 2002, Almany 2004) and pelagic waters (e.g. Ellis & Nash 1997, Köster & Möllmann 2000, Swain & Sinclair 2000). Predation on reef fish in the first 48 hours following settlement can be so heavy that it leads to total recruitment failure (Webster 2002). There is little age or growth data for new recruits of estuarine fishes in this region (but see Robertson & Duke 1990b), thus the definition of new recruits as individuals <20 mm is somewhat arbitrary (Ch. 3). A 20 mm 'new recruit' may have been resident within the estuary for days or weeks (Robertson & Duke 1990b). Consequently it is not entirely clear which predators may prey heavily on new recruits when they first arrive in the estuary, yet heavy predation at this time could have a profound influence on the observed community structure (Steele et al. 1998, Webster 2002).

7.4.6 Conclusions. Within the shallow nursery, a brief switch by the highly abundant minor piscivores could exert massive mortality on new recruits. A very large proportion of the shallow water fish fauna are potential predators, and occasional intense predation events focussed on new recruits have the potential to be major structuring forces that influence the assemblage structure seen within 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), but such events can have a major influence on observed patterns within these systems (e.g. Köster & Möllmann 2000, Swain & Sinclair 2000, Webster 2002). Rather than designing sampling protocols aimed at minimising the 'background' variability, perhaps we should be aiming to capture that variability as a key underlying driving force of the systems we seek to understand.

Chapter 8

General discussion: Piscivory and the functioning of tropical estuarine nurseries

Prior to the present research, our understanding of piscivory within tropical Indo-Pacific estuarine systems was based on a few studies of the general dietary habits of a limited range of mostly large predatory fishes (Blaber 1980, Blaber 1986, Salini et al. 1990, 1998, Haywood et al. 1998, Sheaves & Molony 2000). The role of piscivory was rarely a central focus of these studies. Consequently, the role of predation in structuring tropical estuarine fish assemblages and in the functioning of shallow-water nursery habitats was unclear (Sheaves 2001). The goal of this thesis was to gain a clearer insight into the role of piscivory within shallow tropical estuarine nurseries, and by doing so, to significantly enhance our understanding of the functioning of these important systems.

8.1 Key findings of this research: a new view of estuarine piscivore food webs. This study has provided a markedly different conceptual view to the ‘traditional’ estuarine piscivore food web (Fig. 8.1). Previously, only large primary piscivores were considered as potentially important predators of other estuarine fishes (Fig. 8.1a, b; e.g. Blaber 1980, Salini et al. 1990, Paterson & Whitfield 2000), and there was thought to be few of these in shallow-water habitats (e.g. Paterson & Whitfield 2000). The species considered important in previous studies tended to be mobile fishes susceptible to gill nets (e.g. Blaber 1986, Blaber et al. 1989, Paterson & Whitfield 2000).

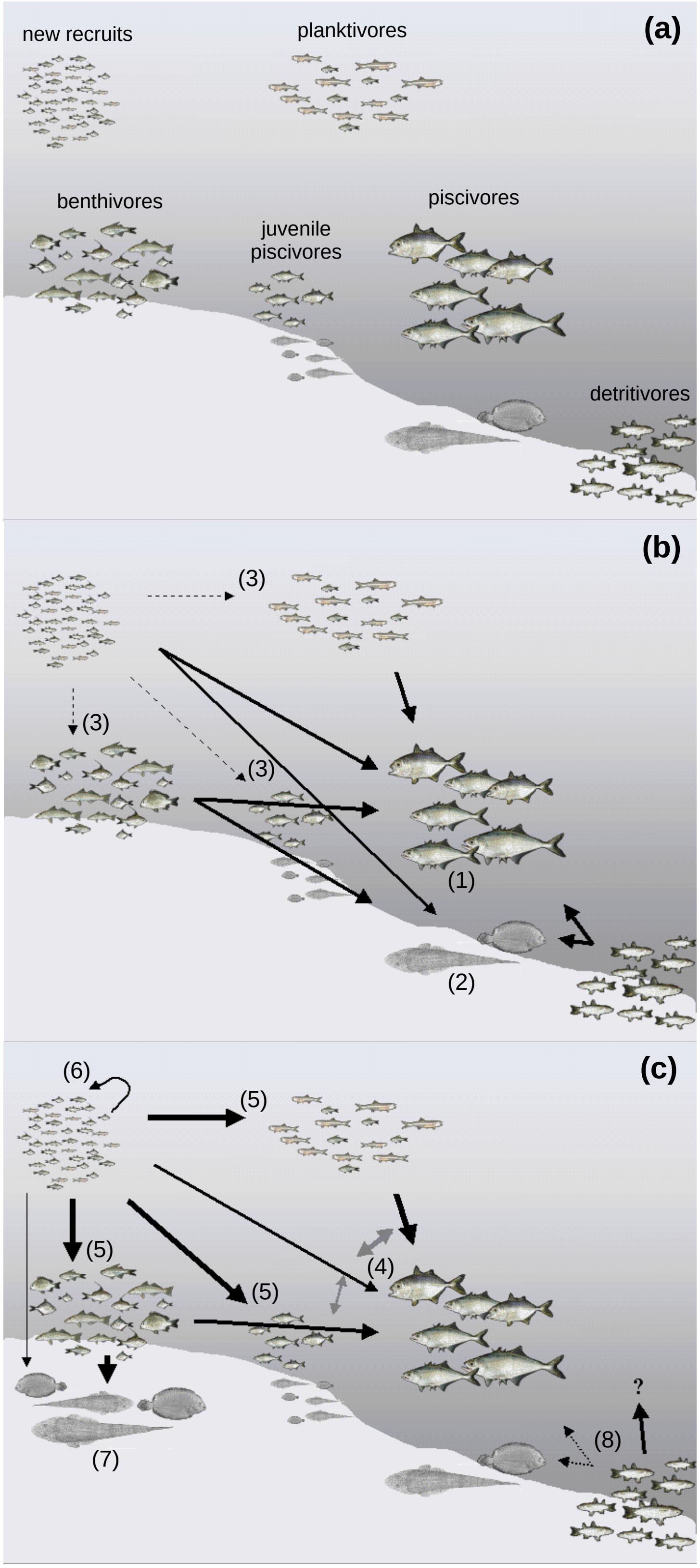


Figure 8.1: A new view of the estuarine piscivore food web. **(a)** major broad functional groups within the shallow-water fish assemblage. These groups are generalised. For example, there are a diversity of functional roles within the broad functional groups such as the 'benthivores' or benthic invertebrate feeders (J. Wilson PhD thesis in prep), and the 'piscivores' (this study). **(b)** the 'traditional' piscivore food web; **(1)** only large major piscivores considered important, thought to be in low abundance in shallow water, **(2)** sedentary or 'resident' major piscivores recorded in relatively low abundance, **(3)** juvenile and minor piscivores considered insignificant. **(c)** A new view of the diverse assemblage of piscivores; **(4)** some large mobile major piscivores (e.g. some carangids) prey on new recruits, but this may be mediated by the availability of alternate prey, particularly pelagic clupeoids, **(5)** juvenile and minor piscivores have the potential to inflict the greatest predation mortality on new recruits, and can do so from a very small size, **(6)** some fish are piscivorous from the time they recruit to the estuary, **(7)** large resident major piscivores are highly abundant in some shallow water habitats and may inflict heavy mortality there, but larger individuals prey little on new recruits, **(8)** few of the piscivores examined preyed on mullet (Mugilidae), despite their high abundances in these habitats.

Because of their size, larger mobile piscivores were presumed to be capable of consuming large numbers of small fish prey (Blaber 1980). While more sedentary or ‘resident’ species such as platycephalids were reported, they were generally only sampled in relatively small numbers (e.g. Salini et al. 1990, Haywood et al. 1998). Few studies considered the potential importance of the occasional consumption of fish prey by other groups such as juvenile piscivores, benthivores and planktivores (e.g. Martin & Blaber 1983). Consequently, these ‘minor’ piscivores were considered insignificant (Fig. 8.1a, b).

This study revealed a piscivore assemblage that is functionally diverse in terms of taxonomic identity, size structure and trophic strategies (Fig. 8.1c). A broad range of the fishes found in shallow-water habitats consume fish prey to some degree (Ch. 3). Some of the large carangids consume large numbers of demersal new recruits, however many of the other large primary piscivores do not (Ch. 3). Many of the carangids also prey heavily on pelagic clupeoids (e.g. Fig. 3.6), and the coexistence of small pelagic and demersal prey may offset the impacts of these predators on the shallow water nursery assemblages. Many predatory fishes begin to consume fish prey from a very small size (Ch. 3), and a broad range of easily overlooked small fishes are potentially important predators of new recruits (Fig. 8.1c).

The low average occurrence of fish in the diet of small and occasional piscivores is a poor reflection of the patterns of predation pressure by these on fish prey (Ch. 4). Most of the time, small and occasional piscivores do not consume fish prey, but occasionally a large proportion of them do. When they do, they consume small new recruits, and it appears these highly abundant predators may switch to target new recruits in response to recruitment events (Ch. 4). Large flathead were found in very high densities in shallow waters (Ch. 5), and the abundance of large piscivores in general may have been considerably underestimated in such habitats due to sampling biases (Rountree & Able 1997, Ch. 5).

Given the abundance and diversity of piscivores in shallow waters, it was not surprising that the tethering experiments provided no evidence that shallow water provides small juvenile fishes with reduced predation pressure relative to the adjacent deeper waters (Ch. 6). In contrast to the proposition that shallow tropical estuarine habitats contain few piscivorous fishes (see review by Sheaves 2001), this study has shown that a very high proportion of the fishes found in shallow water habitats in tropical estuaries are potential predators of new recruits (Ch. 7). Consequently, there is considerable potential for predation on new recruits to be a major structuring force on estuarine fish assemblages, just as it is on coral reef fish communities (e.g. Hixon & Carr 1997, Webster 2002, Webster & Almany 2002). The piscivores with the greatest potential impact within the shallow nursery are themselves small and juvenile fishes utilising shallow water habitats as nurseries (Fig. 8.1c; Ch. 7). Interestingly, very few mullet (Mugilidae) were identified in the diets of the predatory fishes examined in this study (Fig. 8.1c; e.g. Figs. 3.6, 4.3), despite their high abundance in the habitats sampled (Sheaves 2006, Appendix E this study).

8.2 Implications of predation for the flow of energy between estuarine and coastal systems. Since the early 1960's there has been considerable debate about the contribution of estuaries to the productivity of adjacent coastal systems (Teal 1962, Odum 1968 in Nixon 1980, Haines & Dunstan 1975, Haines 1976, Nixon 1980, Deegan 1993). The passive transport of dissolved and particulate nutrients and detritus from productive marsh systems to coastal and offshore waters, termed "outwelling", was considered critical in supporting secondary production of many coastal fisheries (Odum 1968 in Nixon 1980). This contribution of productivity has been used almost universally to justify the importance and protection of marsh and estuarine systems (Nixon 1980). The transport of nutrients between estuarine and coastal systems is now recognised as a complex and dynamic process (Boto & Bunt 1981, Moran et al. 1991, Ford et al. 2005, Webster et al. 2005), and the general model of 'outwelling' appears too simplistic (Nixon 1980, Kneib 1997, Ford et al. 2005). Regardless of the direction of the overall net flux of nutrients and energy, material transport across ecosystem boundaries may be a key driver of ecosystem trophodynamics (Zhang et al. 2003, Sheaves 2005).

The role of biological transport through the migrations of animals between systems was generally considered insignificant relative to the quantities of dissolved and particulate organic matter transported by the massive volumes of moving water (Nixon 1980, Day et al. 1989). However, dissolved nutrients and those within detritus are of relatively low nutritive value, are generally assimilated through bacterial pathways or other organisms low in the food chain, or are lost to higher trophic levels through sedimentation (Nixon 1980). Consequently, although the passive transport of energy and nutrients between estuarine and coastal systems may be large in magnitude relative to that via animal migrations (Nixon 1980), the high value ‘available’ energy and nutrients transported as prey biomass may represent a disproportionately large contribution to higher trophic levels such as fisheries species (Deegan 1993).

The significance of energy and nutrient transport by fish migrations is well recognised in salmonid spawning streams along the Pacific coast of North America (Ben-David et al. 1998, Helfield & Naiman 2001, Zhang et al. 2003, Johnston et al. 2004, Koyama et al. 2005). Pacific salmon migrate from feeding grounds in the ocean to their natal freshwater streams where they spawn and then die (Helfield 2002). Predation and decomposition of post-spawn salmon carcasses represents a considerable input of marine-derived nutrients to both instream production (Zhang et al. 2003, Johnston et al. 2004), and to the riparian vegetation and associated food webs adjacent to the spawning streams (Ben-David et al. 1998, Helfield & Naiman 2001, Koyama et al. 2005). The effects of this ‘fertiliser’ on instream production may provide considerable short-term benefits for the newly hatched salmon fry (Johnston et al. 1990, Zhang et al. 2003). Additionally, nutrient subsidies which boost the production of the riparian zone may have long-term benefits of enhancing the habitat quality of spawning and rearing streams for future generations (Helfield & Naiman 2001).

The potential significance of fish migrations in the energy budgets and nutrient cycles linking coastal and estuarine systems have recently been recognised (e.g. Deegan 1993, Kneib 1997, Sheaves & Molony 2000, Sheaves 2005). However, perhaps due to findings that mortality of some juvenile fishes utilising estuarine nursery grounds is low (e.g. Deegan 1990)(and the widespread belief that this is a global phenomenon), it is generally considered that the net effect of the juvenile use of estuarine nurseries is the transport of estuarine productivity to coastal or offshore systems (Deegan 1993). The significance of the transport of energy and nutrients by new recruits from coastal waters into estuaries has received little direct consideration. Regardless of the net result of cyclical fish migrations or movements, individual components such as the recruitment of juveniles into the nursery or migration of sub-adults offshore may still represent significant subsidies of energy and nutrients transported across ecosystem boundaries (e.g. Sheaves & Molony 2000, Sheaves 2005).

In one of the few studies to attempt to directly quantify nutrient and energy transport between coastal adult habitats and estuarine nurseries by fishes, Deegan (1993) estimated that the movement of gulf menhaden (*Brevoortia patronus*) resulted in a net export of energy and nutrients from estuaries. Deegan (1993) concluded that fish migration is an important component of the overall export of estuarine productivity to coastal systems (Fig. 8.2). Mortality during estuarine residence is critical in controlling the magnitude of the flux (Deegan 1993, Fig. 8.2b). Deegan (1993) noted that if the juvenile menhaden had suffered the equivalent of an additional 30 days of mortality during their 270-day estuarine residence, the result would have been a net balance, or zero net flux of nutrients and energy between the estuary and coastal waters (Fig. 8.2c).

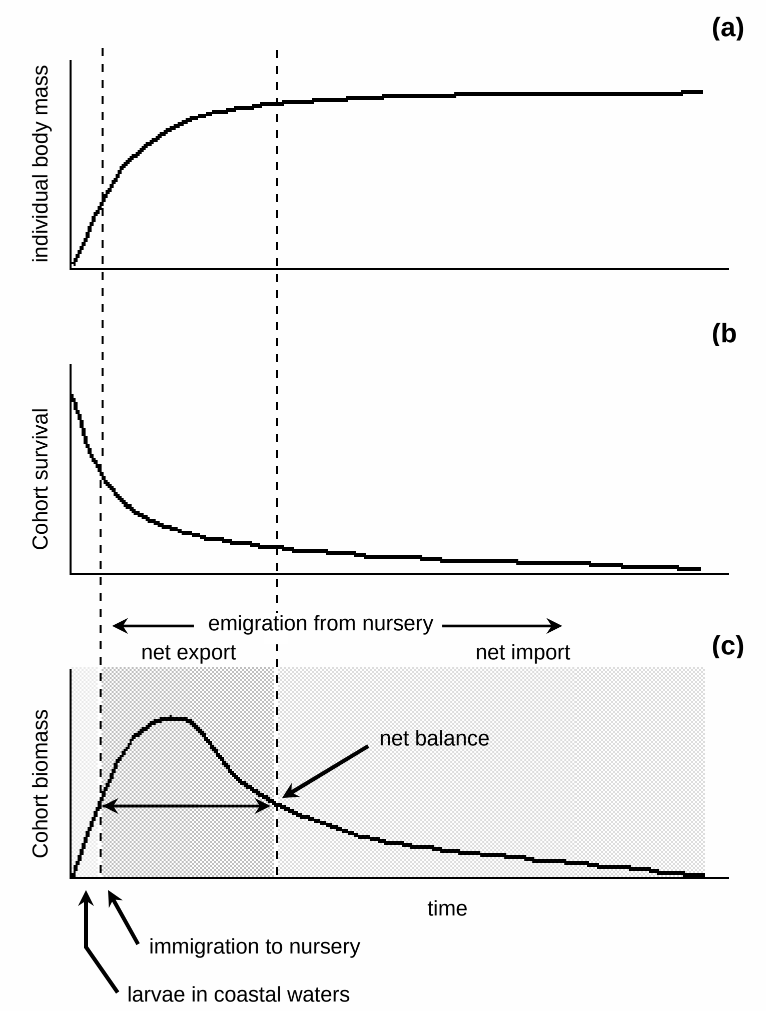


Figure 8.2: Transport of energy and nutrients (biomass*) via the migration of fishes between coastal and estuarine systems. The combination of individual growth (a) and cohort mortality (b) rates determine cohort biomass (c)(Adapted from Yanez-Arancibia et al. 1994). The biomass accumulated by larval fishes in coastal waters (light shading) represents an input of energy and nutrients into the estuary at the time of recruitment (immigration). Through time, cohort mortality (b) overcomes individual growth (a) such that cohort biomass peaks and falls (c). If sub-adults emigrate from the estuary prior to cohort biomass falling to the biomass at immigration (dark shading) there is a net export of biomass. If the biomass of the emigrating cohort falls below that of the immigrating juveniles (medium shading), the result is a net import of biomass from coastal waters into the estuary. *Note that relative nutrient content per unit biomass changes though ontogeny (Deegan 1993) and thus biomass is not a perfect proxy for nutrient transport. However, conceptually the model is the same if nutrients or energy are substituted for individual (a) and cohort (c) biomass.

While the findings of Deegan (1993) highlight the potential importance of fish migrations in the transport of energy and nutrients across ecosystem boundaries, scrutiny of the data presented suggests significant potential for a net transport of energy and nutrients into estuarine systems by the migrations of juvenile menhaden, in contrast to the conclusions of the study. An additional 30 days mortality is the equivalent of the measured average daily instantaneous mortality rate (Z, Deegan 1990) increasing by 11.1 % over the 270-day residence time (30/270*100). Thus, an increase in Z from 0.007 to 0.008 (1982) and from 0.018 to 0.020 (1983) during the two years of the study would have resulted in zero net flux of energy and nutrients (Deegan 1993, Fig. 8.2c). The required increase is considerably smaller than either the measured inter-annual variability in mortality rate (0.007 Vs 0.018), or the standard errors in individual mortality rate estimates (range 0.0023 – 0.0071) (Deegan 1990). Consequently, the migration of menhaden between estuarine and coastal systems could easily result in a net transport of energy and nutrients from the coast to the estuary, particularly at times or locations of high juvenile mortality within the estuarine nursery (Fig. 8.2).

Estuarine fish faunas around the world are dominated by ‘transient’ species which are spawned offshore and utilise estuarine systems as juvenile nurseries before returning to the adult populations (Yanez-Arancibia 1985, Deegan 1993, Kneib 1997). Early juvenile stages of fishes typically suffer very high levels of mortality (Fig. 8.2b, Yanez-Arancibia et al. 1994, Sogard 1997), and predation is a major source of natural mortality (Carr & Hixon 1995, Sogard 1997). Mortality estimates were not undertaken as part of the present study. However, given that more than half of the fishes encountered by a cohort of new recruits within some shallow water habitats are potential predators (Ch. 7), there is great potential for considerably higher mortality on new recruits in tropical estuarine systems than that reported for temperate systems (e.g. Deegan 1990).

Estimates of the magnitude of inputs from new recruits relative to the nutrient budgets of estuarine systems are beyond speculation from the data presented in this study, and beyond the current level of understanding of the functioning of these systems. However it seems reasonable to conclude that regardless of the overall net transport between estuarine and coastal waters, the recruitment and subsequent predation on new recruits into and within estuarine systems represents a significant contribution of coastal productivity to these systems. The nutrient subsidy may enhance the nursery ground value of estuaries (Johnston et al. 1990, Helfield & Naiman 2001, Zhang et al. 2003). Returns for parental investment in reproduction may be improved if a large proportion of the offspring that are eaten contribute nutrients to the nursery ecosystem which the surviving offspring are part of during their juvenile phase, analogous to the contribution of dying post-spawn salmon to the rearing streams of their offspring (Helfield & Naiman 2001). Even if there are not strong feedback loops within estuarine food webs to deliver nutrients from predated new recruits back to other members of their cohort (e.g. via detrital pathways), successive pulses of recruitment may provide important nutrients for previous cohorts capable of preying on new recruits (Ch. 3 & 4). Rather than being places of low predation mortality, heavy predation on new recruits within tropical estuarine nurseries may in fact enhance the nursery value of these habitats and be a significant process in maintaining the productivity of these systems.

8.3 Implications for the refuge paradigm and estuarine nursery ground functioning.

Does this all mean that shallow water estuarine habitats do *not* provide juvenile fishes with a refuge from predation? Few studies, including much of this one (except Ch. 6), have been able to compare processes such as predation between potential nursery habitats (Rountree & Able 2006). Thus direct assessments of the value of shallow water nurseries are scarce. The tethering study showed no evidence of reduced predation pressure in shallow habitats relative to the adjacent deeper waters (Ch. 6). Additionally, a large proportion of the fishes within shallow water habitats are piscivorous (Ch. 7). Despite these two findings indicating high predation potential in shallow waters, many of the small and juvenile fishes characteristic of estuarine fish faunas in this region (Robertson & Duke 1987, Blaber et al. 1989, Haywood et al. 1998, Sheaves 2006) show a strong affinity for shallow water habitats (e.g. Fig. 6.2 this study, R. Johnston PhD thesis in prep). It seems then, that if predation is an important process in structuring the distribution of small and juvenile fishes in tropical estuaries, then it does not operate through the simplistic mechanism implied by the shallow-water refuge paradigm.

The occupation of shallow water habitats by small and juvenile fishes appears to be a global phenomenon (Shenker & Dean 1979, Boesch & Turner 1984, Robertson & Duke 1987, Ruiz et al. 1993, Paterson & Whitfield 1996, Barletta et al. 2003, Krumme et al. 2004), despite differences in faunal compositions (Blaber 2000), diversity within piscivore assemblages (Hartman & Brandt 1995, Ch. 3 & 4 this study), and structural differences in the range of habitats (Kneib 1997, Smith & Hindell 2005, Sheaves 2005). So why do small fishes occupy shallow waters? The shallow-water refuge paradigm is based on the tenet that predation risk decreases as a function of decreasing water depth and increasing body size, leading to size-structured depth distributions of vulnerable fishes (Ruiz et al. 1993). Because of the general positive relationship between prey and predator size (Scharf et al. 2000, Layman et al. 2005), for any given depth larger individuals should gain greater refuge than smaller ones (Ruiz et al. 1993). Thus, the refuge paradigm implies that the water depths occupied by small fish restrict or prevent access of their larger predators (e.g. Cain & Dean1976, Boesch & Turner 1984, Rozas & Hackney 1984, Paterson & Whitfield 2000).

Some authors have hypothesised that small fishes may gain refuge in shallow waters because larger fishes are at greater risk from predation when in these habitats, primarily from terrestrial or avian predators (Ruiz et al. 1993, Paterson & Whitfield 2000, Linehan et al. 2001). While avian predation may be a significant risk for fishes occupying shallow waters in some parts of the world (Whitfield & Blaber 1978, Whoriskey & Fitzgerald 1985, Dieperink 1994, Crowder et al. 1997), this hypothesis contradicts the basis of the shallow-water refuge paradigm (Ruiz et al. 1993). It also seems counter-intuitive that larger fishes should be more vulnerable to avian predators than smaller ones because a wider range of avian predators can consume small fish than large ones (Layman et al. 2005). Furthermore, in north-eastern Queensland avian predation does not appear to be as significant as in other parts of the world (Blaber 1980, Ch. 6 this study).

The shallow waters occupied by many small and juvenile fishes in this region (Fig. 6.2) are too deep to physically exclude the majority of their fish predators (Ch. 3), and high densities of a broad size range of piscivores have been recorded in these habitats (Ch. 5 & 7). The diversity within the piscivore assemblage and the importance of predation on new recruits highlights the inadequacy of the shallow-water refuge paradigm for explaining the distribution patterns of small and juvenile fishes in tropical estuaries. This does not mean that predation plays no role in the distribution patterns of fishes within tropical estuaries, but rather that the idea that shallow water = few piscivores = refuge from predation is too simplistic for these complex and dynamic systems.

Sublethal effects of predation, such as the stimulation of energetically expensive defensive strategies, may be a significant mechanism through which predation can influence prey behaviours (Abrams 1993, Preisser et al. 2005). Consequently, there may have to be little difference in the actual consumption of fish prey between shallow and deep habitats (e.g. Ch. 6) to cause the observed distribution patterns of small fishes. If sublethal effects are less costly in shallow than in deep water, then predation may be a significant factor driving the shallow water distribution, even if actual predation mortality differs little across the depth range (Abrams 1993, Preisser et al. 2005). For example, the cost of vigilance may be less in shallow waters because there are fewer directions from which a predator can approach (Hixon & Carr 1997). In such circumstances, small fishes in shallow waters could spend less time monitoring for predators and more time foraging.

Fish distributions and habitat selection must logically be based on a trade-off between the profitability and cost of the utilisation of various habitats. While the relative importance of foraging profitability and predation risk have been widely studied elsewhere, with conflicting results (e.g. Cerri & Fraser 1983, Boesch & Turner 1984, McIvor & Odum 1988, Rozas & Odum 1988, Connolly 1994, Miltner et al. 1995, Levin et al. 1997, Halpin 2000, Laegdsgaard & Johnson 2001, Minello et al. 2003), there is little current knowledge of the distribution patterns of the prey resources utilised by the shallow-water tropical estuarine fish fauna. Obviously the distribution of available prey may play a large role in the habitat use of small and juvenile fishes in tropical estuaries, and future research is needed in this area.

The potential role of hydrodynamics on fish distributions has received little attention (Allouche 2002), however the relative costs of maintaining position against water movement may be a significant factor in size-related depth distributions (Ruiz et al. 1993). Tidal currents in deeper waters may simply be too strong or too energetically expensive for small fishes to maintain or control their position. If food resources and predation risk are spatially patchy, then the cost of movement between patches or habitats may be a significant factor in determining fish distributions (Sheaves 2005, Rountree & Able 2006). Additionally, for fishes that utilise a mosaic of connected habitats, the patterns observed in one habitat may be driven by processes occurring in another. Thus the distribution of fishes in shallow waters may be related to the trade-off between cost and benefit of accessing or moving between alternate feeding or refuge habitats (Sheaves 2005).

8.4 Challenges and directions for future research. Estuaries can be difficult environments in which to work (Kneib 1997, Rozas & Minello 1997, Blaber 2002). Many of the challenges relate to the reliance on a range of sampling tools that have widely varying and often unknown efficiencies (Kneib 1997, Rozas & Minello 1997). This is particularly relevant for examination of factors such as the relative importance of different members of a diverse piscivore assemblage (Ch. 7). When the fishes of interest range from small fishes susceptible to gears such as seine nets (Kneib 1997, Rozas &

Minello 1997) up to large mobile individuals that may only be captured by essentially non-quantitative sampling tools such as gill nets (Smith & Hindell 2005), meaningful comparisons of the relative abundance of different groups are extremely challenging, and issues such as the relative predation impacts of these fishes in different habitats are difficult to resolve (Rountree & Able 2006).

Many of the carangids examined in this study can be observed feeding in large schools (Ch. 5). They may prey heavily on a range of fish prey including new recruits (Ch. 3), and periodically gain access to shallow water habitats (Blaber et al. 1985). Consequently, carangids are potential powerhouses in terms of total predation on small fishes in estuarine systems, yet quantifying their abundance to estimate their relative impact is extremely difficult. New technologies such as side-scan sonar capable of identifying species and providing quantitative abundance and biomass estimates should be important tools in future research on the trophic dynamics of tropical estuarine systems.

Detailed dietary studies such as this one can provide considerable insights into the functioning of estuarine systems. In particular, this study has highlighted the importance of examining details of the variability in dietary habits in clarifying important processes that have been missed by previous studies which examined only pooled ‘average’ diets (Ch. 4). Average levels of processes such as predation may not be indicative of the importance of those processes (Edwards et al. 1982, Köster & Möllmann 2000, Sheaves 2005), and future research should seek to capture such variability as a fundamental driving force behind observed patterns, rather than design projects to ‘overcome’ this variability.

As discussed earlier, the distribution patterns and dynamics of the prey resources of small and juvenile fishes requires further investigation, as does the potential importance of hydrodynamics in shaping the distribution patterns of tropical estuarine fishes. Understanding the processes that drive the patterns of distribution and habitat use of juvenile fishes within estuarine nurseries is not only critical to the understanding of the importance of particular habitats in the overall functioning of these systems, but is also vital information for the managers and policy makers charged with protecting these systems into the future.

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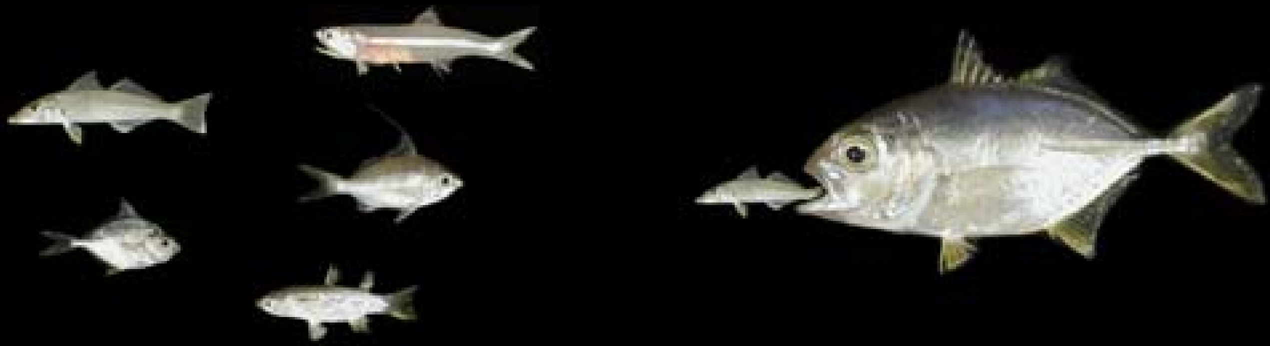
Zimmer-Faust RK, Fielder DR, Heck KL, Coen LD, Morgan SG (1994) Effects of tethering on predatory escape by juvenile blue crabs. Mar Ecology Prog Ser 111:299-303



Otolith catalogue of common coastal and estuarine fishes of north-eastern Queensland, Australia

Ron Baker

Appendix A

Otolith catalogue of common coastal and estuarine fishes of north-eastern Queensland, Australia

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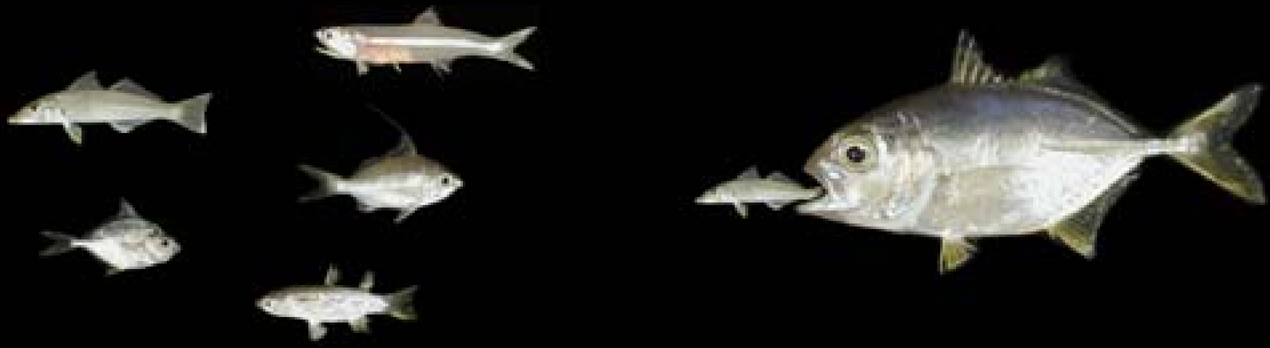
Available online at:

http://www.jcu.edu.au/school/mbiolaq/ind_labs/estecol/



Otolith catalogue of common coastal and estuarine fishes of north-eastern Queensland, Australia

Ron Baker

Appendix A

Otolith catalogue of common coastal and estuarine fishes of north-eastern Queensland, Australia

Introduction

This catalogue provides photographs of the sagittal otoliths of a range of coastal and estuarine fishes common in the Townsville region of north-eastern Queensland, Australia. Studies utilising gut content analysis to examine trophic dynamics are limited by the digestion process; many prey items are rapidly digested beyond identification making quantification of dietary composition difficult. Teleost fishes consumed by predators may be rapidly digested making them unrecognisable from external morphological features. However hard parts such as bones and otoliths are much more resilient to digestion and have regularly been used to aid in the identification of partially digested remains (e.g. Jobling & Breiby 1986, Scharf et al. 1997). As can be seen on the following pages, otolith morphology is often species- or genera-specific, allowing confident identification to at least a generic level.

This catalogue can be used to identify fishes from otolith remains found in the digestive tracts or faeces of predators, sediment samples or fossils. Otolith-weight/fish length relationships are also provided for a number of the more common taxa. Such relationships have been used to estimate prey size from otolith remains (e.g. Baker & Sheaves 2005), however caution must be used with this approach as otoliths exposed to acidic digestive fluids will begin to dissolve and thus may provide biased size estimates (Jobling & Breiby 1986, discussed below).

The 28 taxa presented combined represent more than 90% of the total catch of fishes sampled with 12mm seine nets over 3 years from 9 estuaries in the Townsville region (Sheaves 2006). Similarly, these species comprised more than 88% of the >2800 fish prey found in the diets of more than 40 taxa of predatory estuarine fishes sampled from the region (Baker & Sheaves 2005).

Otolith preparation

Sagittal otoliths were removed and placed in bleach (sodium hypochlorite) for a few minutes to help remove the otic membrane and any other tissue. Otoliths were then rinsed in alcohol and allowed to dry before storage. Photographs were taken using a Nikon Coolpix 990 camera mounted on a dissecting microscope. Efforts were made to include pictures across a size range to allow for ontogenetic changes in otolith morphology. Each otolith was photographed from both the left and right sides, and dorso-ventrally to provide a complete picture of the 3-dimensional shape of each otolith.

Otolith-weight/fish length regressions

Individuals encompassing the size range commonly encountered in the diets of predatory fishes were collected from a number of estuaries in the region. Otoliths were removed and prepared as for the photography. Fish were measured (fork length [FL] to the nearest mm) and the otoliths weighed (to the nearest 0.00001g).

An equation to estimate FL(mm) from otolith weight (g * 0.00001) was derived using the curve fit function in SPSS and Excel (Table A1). Although fitting the power curve may have a sound theoretical basis, power curves for several species provided a poor fit at the upper end of the size range, usually significantly underestimating FL. In such cases, third-order polynomials (cubic) usually provided a better fit. In each instance, the best fit was determined by examination of the residuals. When adequate curves could not be fitted to the entire data range, the relationship was broken into segments, and curves were fitted to each separately. Where several species within a genus have otoliths with similar morphology such that species may not always be confidently separated (e.g. *Sillago* spp.), genus-level regressions were also calculated by combining data for all species within the genus. Similarly, small individuals (<20-30 mm) of several genera are difficult to identify to species (e.g. *Leiognathus* spp., *Sillago* spp.). Therefore the individual species relationships included small individuals identified as juveniles at the genus level (e.g. *Sillago* juveniles) and these data were used in each of the species relationships for that genus.

Table A1: Summary of otolith weight – fish length relationships of common coastal and estuarine fishes of north-eastern Queensland, Australia. Used to estimate prey fish size from otoliths found in stomach contents of predatory fish.

		data range			
Taxon	n	FL (mm)	otolith weight (*0.00001g)	regression equation; FL (mm) =	R^2
Leiognathus decorus	59	10 - 57	3 - 134	$5.5519164127\ \text{oto w}^{0.4738498130}$	0.977
L. equulus	18	12 - 71	4 - 161	$6.0064330816\ \text{oto w}^{0.4777737386}$	0.992
L. splendens	22	15 - 44	3 - 62	$0.4937052933\ \text{oto w} + 13.4678631812$	0.951
Leiognathus spp.	96	9 - 71	3 - 161	$0.0000202066\ \text{oto w}^3 - 0.005655363\ \text{oto w}^2 + 0.7735058613\ \text{oto w} + 9.5664096278$	0.978
Secutor ruconius	190	14-42	5 - 245	$0.0000014511\ \text{oto w}^3 - 0.0009648890\ \text{oto w}^2 + 0.2648799048\ \text{oto w} + 13.7895404081$	0.947
Sillago analis	175	28 - 219	40 - 9720	$4.6647586643\ \text{oto w}^{0.4135860798}$	0.984
S. ciliata	141	41 - 250	180 - 15590	$3.9265989417\ \text{oto w}^{0.4276622977}$	0.961
S. maculata	242	24 - 105	50 - 1860	$4.6529469169\ \text{oto w}^{0.4084308713}$	0.961
S. sihama <75 mm FL	285	14 - 74	5 - 870	$0.0000001357\ \text{oto w}^3 - 0.0002273608\ \text{oto w}^2 + 0.1627845325\ \text{oto w} + 17.5894301214$	0.952
Sillago juveniles	61	13 - 25	1 - 39	$0.3057709993\ \text{oto w} + 13.5646701717$	0.906
Sillago spp. otolith weight ≤0.00500g	505	13 - 61	1 - 499	$0.0000004768\ \text{oto w}^3 - 0.0004758133\ \text{oto w}^2 + 0.2082540498\ \text{oto w} + 15.7812485390$	0.973
Sillago spp. otolith weight >0.00500g, ≤0.02000g	335	55 - 109	500 - 1999	$0.0000000062\ \text{oto w}^3 - 0.0000325061\ \text{oto w}^2 + 0.0777068266\ \text{oto w} + 27.0979715689$	0.921
Sillago spp. otolith weight >0.02000g	81	99 - 250	2000 - 15590	$0.000000000004\ \text{oto w}^3 - 0.000000577124\ \text{oto w}^2 + 0.019654504145\ \text{oto w} + 68.204630914029$	0.968
Ambassis telkara	60	19-59	46 - 910	$0.0000000941\ \text{oto w}^3 - 0.0001729524\ \text{oto w}^2 + 0.1270204739\ \text{oto w} + 15.6583275180$	0.975
Acentrogobius viridipunctatus	66	15 - 42	10 - 230	$0.0000003771\ \text{oto w}^3 - 0.0003508539\ \text{oto w}^2 + 0.1749409187\ \text{oto w} + 15.7413639960$	0.858
Gerres filamentosus	21	15 - 62	3 - 532	$0.0000005855\ \text{oto w}^3 - 0.0006268137\ \text{oto w}^2 + 0.2528649076\ \text{oto w} + 17.2034507989$	0.991
Clupeidae	30	21 - 91	4 - 220	$0.0000085417\ \text{oto w}^3 - 0.0035691253\ \text{oto w}^2 + 0.6885894142\ \text{oto w} + 21.3706790178$	0.986
Stolephorus spp.	32	23 - 77	3 - 374	$18.4044032700\ \text{oto weight}^{0.2234651748}$	0.904
Mugilidae	167	18 - 92	20 - 500	$-0.0000000077\text{oto w}^3 - 0.0000249091\text{oto w}^2 + 0.1238463453\ \text{oto w} + 30.6567100629$	0.911

Validity of otolith-weight/fish-length relationships

Prey fish otoliths exposed to acidic digestive fluids in the stomachs of fishes will gradually erode and thus those exposed for long periods may be unreliable for estimating prey size (Jobling & Breiby 1986). In using the otolith weight – prey length relationships to estimate the length of fish prey from otolith remains in the stomachs of predatory estuarine fishes (Baker & Sheaves 2005), a number of precautions and validations were undertaken:

(1) otoliths showing obvious signs of digestion such as loss of fine structural details were not used to estimate prey length,

(2) comparison of length estimates and measurements from 27 fish prey in advanced stages of digestion and not morphologically identifiable, yet sufficiently intact to obtain length measurements, and with otoliths still encased within the otic capsule, revealed a high degree of accuracy in the length estimates from these prey (estimated length = 1.02*measured length, R^2=0.93),

(3) there was little difference between the upper and lower boundaries of the predator-prey length relationships described by quantile regression (Scharf et al. 1998) for scatter plots including and excluding prey lengths estimated from otoliths free of the otic capsule but showing no signs of digestion.

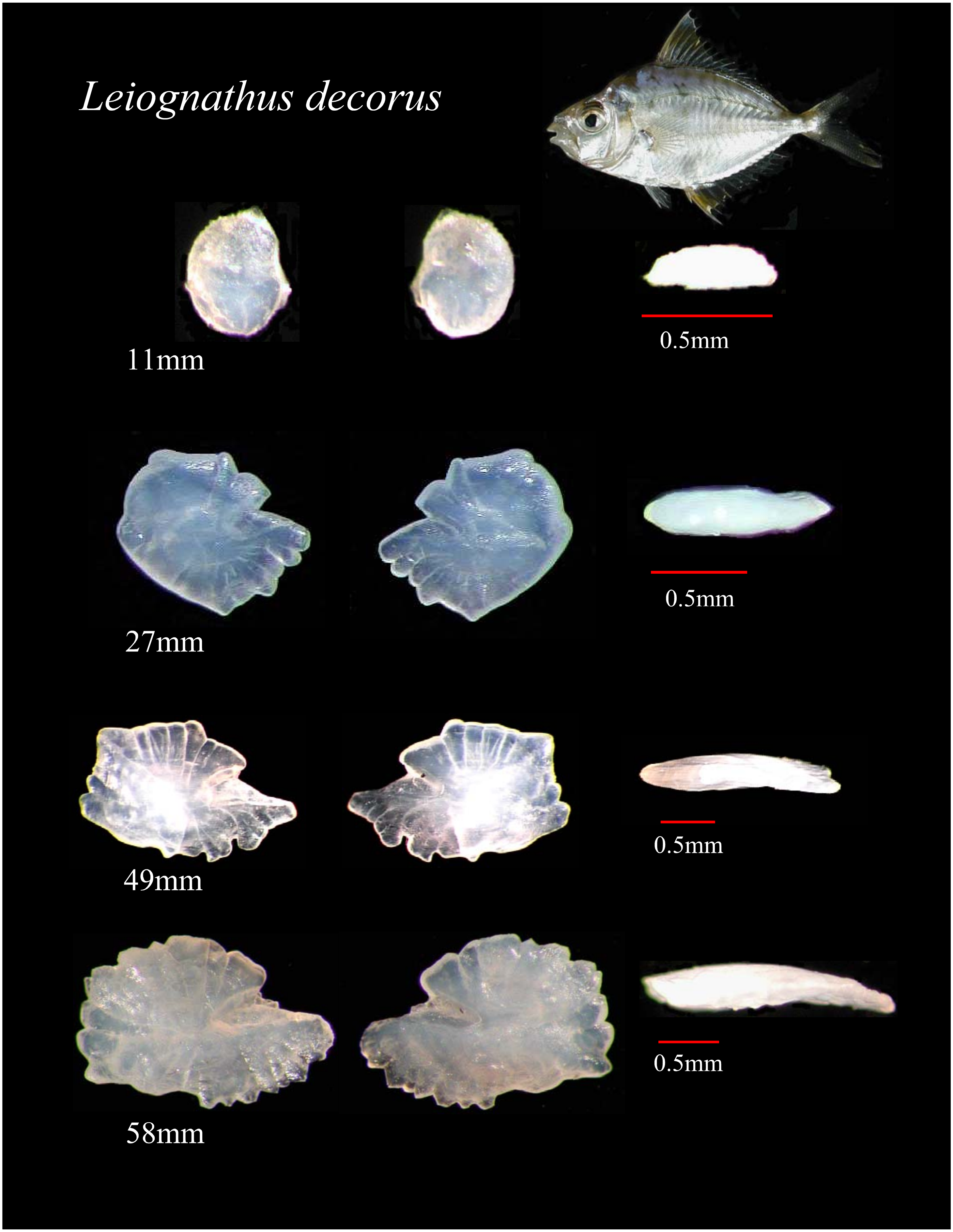
Thus, estimates of fish prey length from otoliths encased in the otic capsule, or exposed to but showing no signs of digestion were considered reliable. It is strongly recommended that similar precautions and validations are undertaken before applying either the otolith-weight/fish-length relationships provided in this catalogue, or this technique in general, for estimating prey size from otolith remains. It is furthermore recommended that before use of any of the relationships provided in this catalogue to estimate prey size in other studies, that the relationships are validated with a sample of individuals from the locations from which predators were collected, as such relationships are likely to vary through time and with geographic location.

Otolith catalogue contents

- Leiognathidae[#]
    - *Leiognathus decorus*[#]
    - *L. equulus*[#]
    - *L. splendens*[#]
    - *Gazza minuta*
    - *Secutor insidiator*
    - *S. ruconius*[#]
- Sillaginidae[#]
    - *Sillago analis*[#]
    - *S. ciliata*[#]
    - *S. maculata*[#]
    - *S. sihama*[#]
- Ambassidae
    - *Ambassis nalua*
    - *A. telkara*[#] *
- Gobiidae
    - *Acentrogobius viridipunctatus*[#]
    - *Psammogobius biocellatus*
- Gerreidae
    - *Gerres filamentosus*[#]
- Clupeidae[#]
    - *Herklotsichthys* spp.
    - *Sardinella* spp.
- Engraulidae
    - *Stolephorus* spp.[#]
- Hemiramphidae
    - *Hyporhamphus affinis*
- Atherinidae
    - *Hypoatherina temmenickii*
- Mugillidae[#]
    - *Mugil georgii*
    - *Liza subviridus*
    - *L. vagiensis*
    - *Valamugil buchanani*
    - *V. cunnesius*
- Platycephalidae
    - *Platycephalus arenarius*
    - *P. fuscus*
- Paralichthyidae
    - *Pseudorhombus arsius*

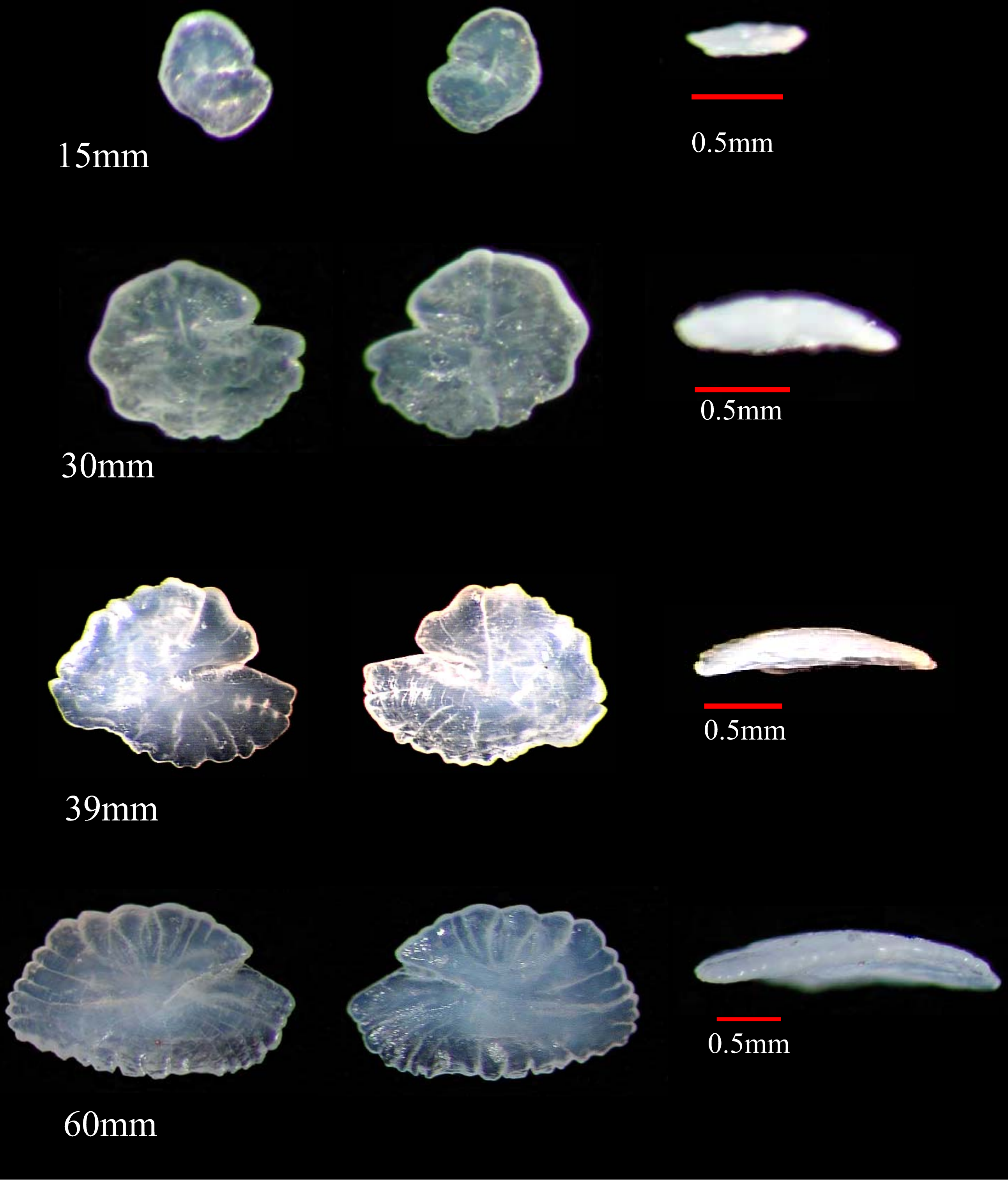
[#] Taxa for which otolith weight – fish length relationships are provided

******A. telkara* has previously been identified as *A. gymnocephalus* and *A. vachelli* by other authors (Komori 2001)



Leiognathus decorus

Leiognathus equulus



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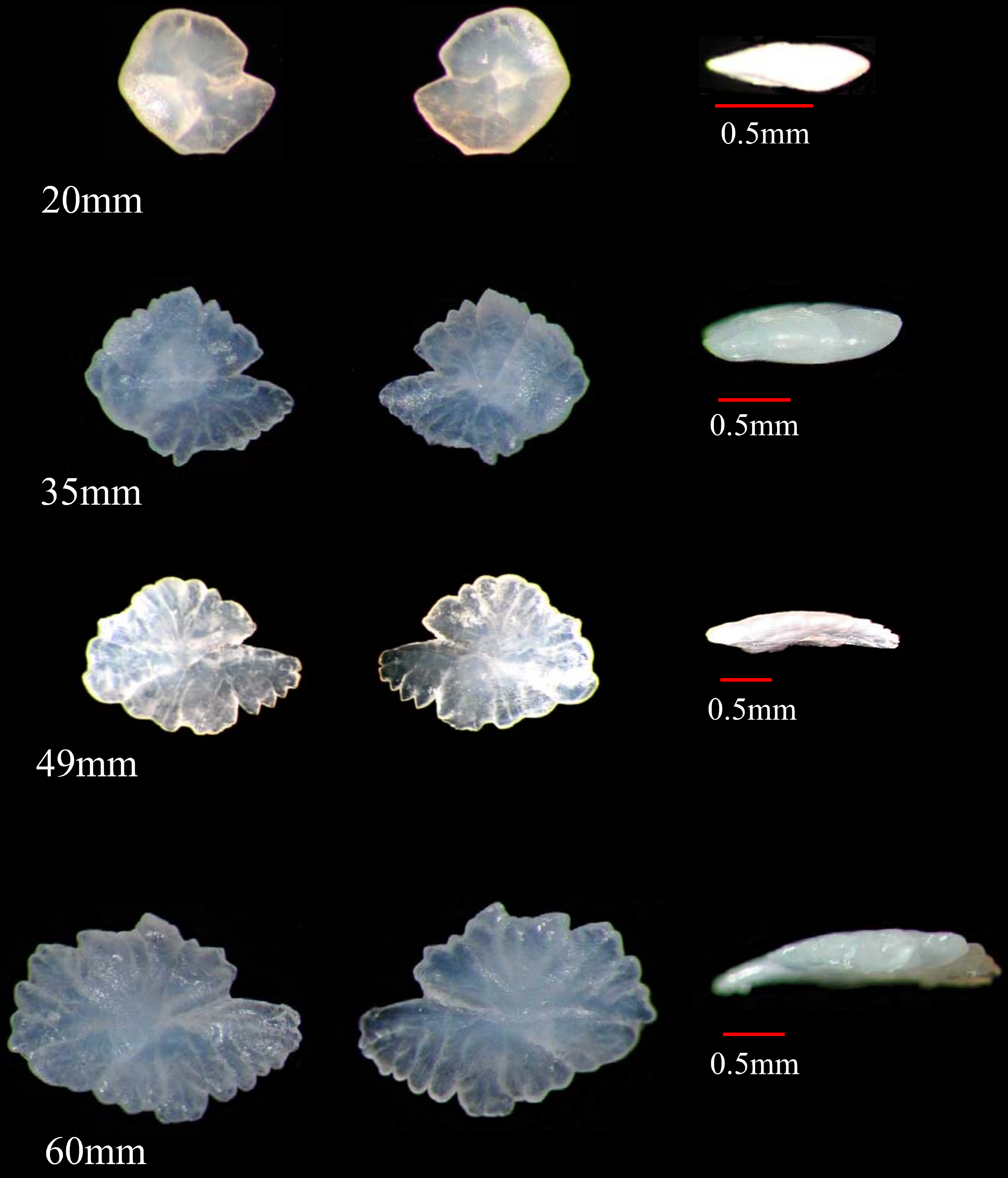
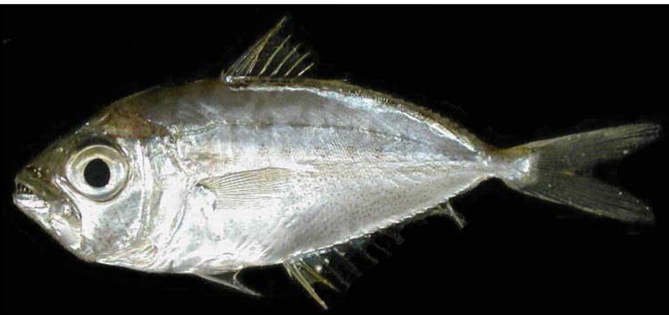


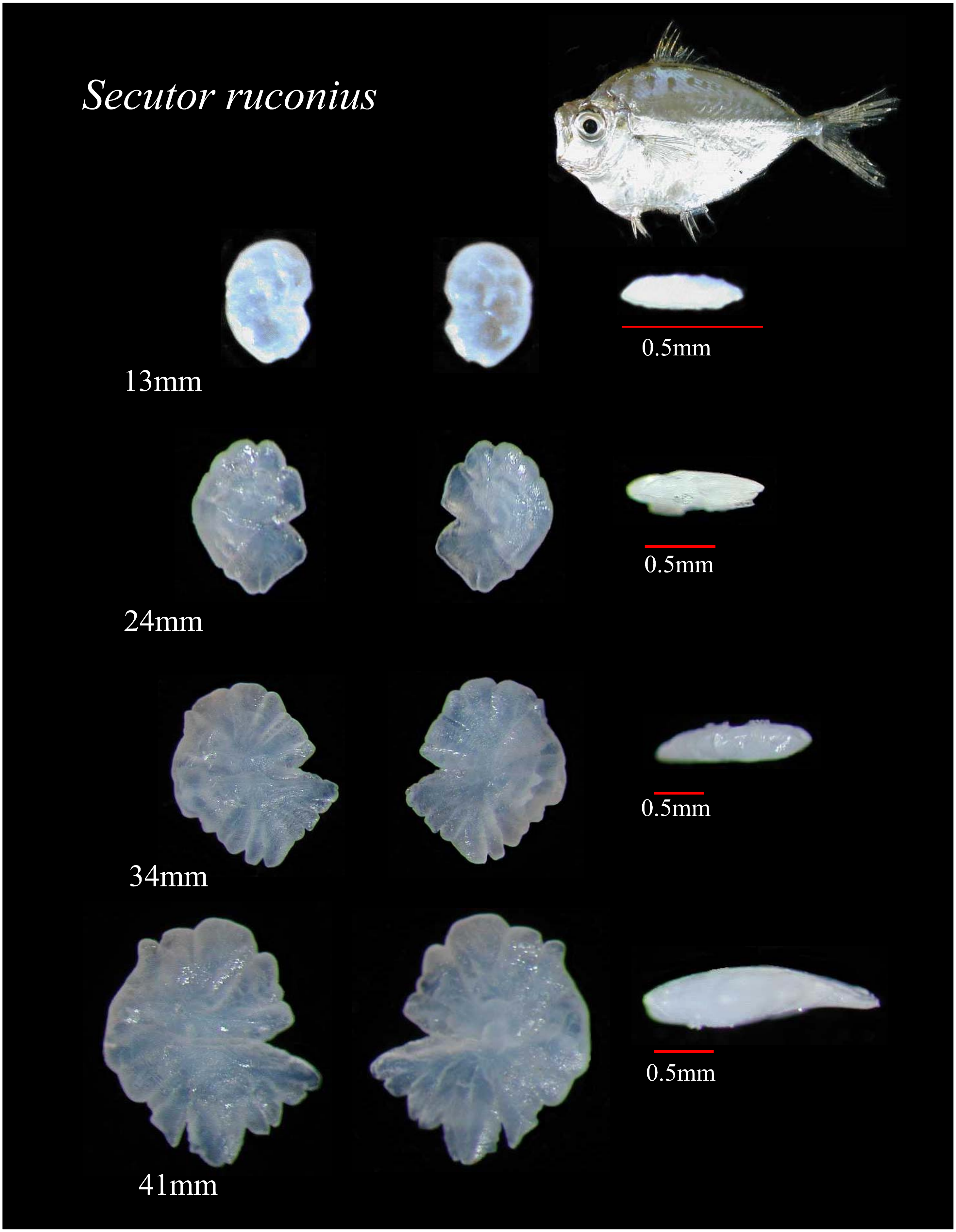
Gazza minuta



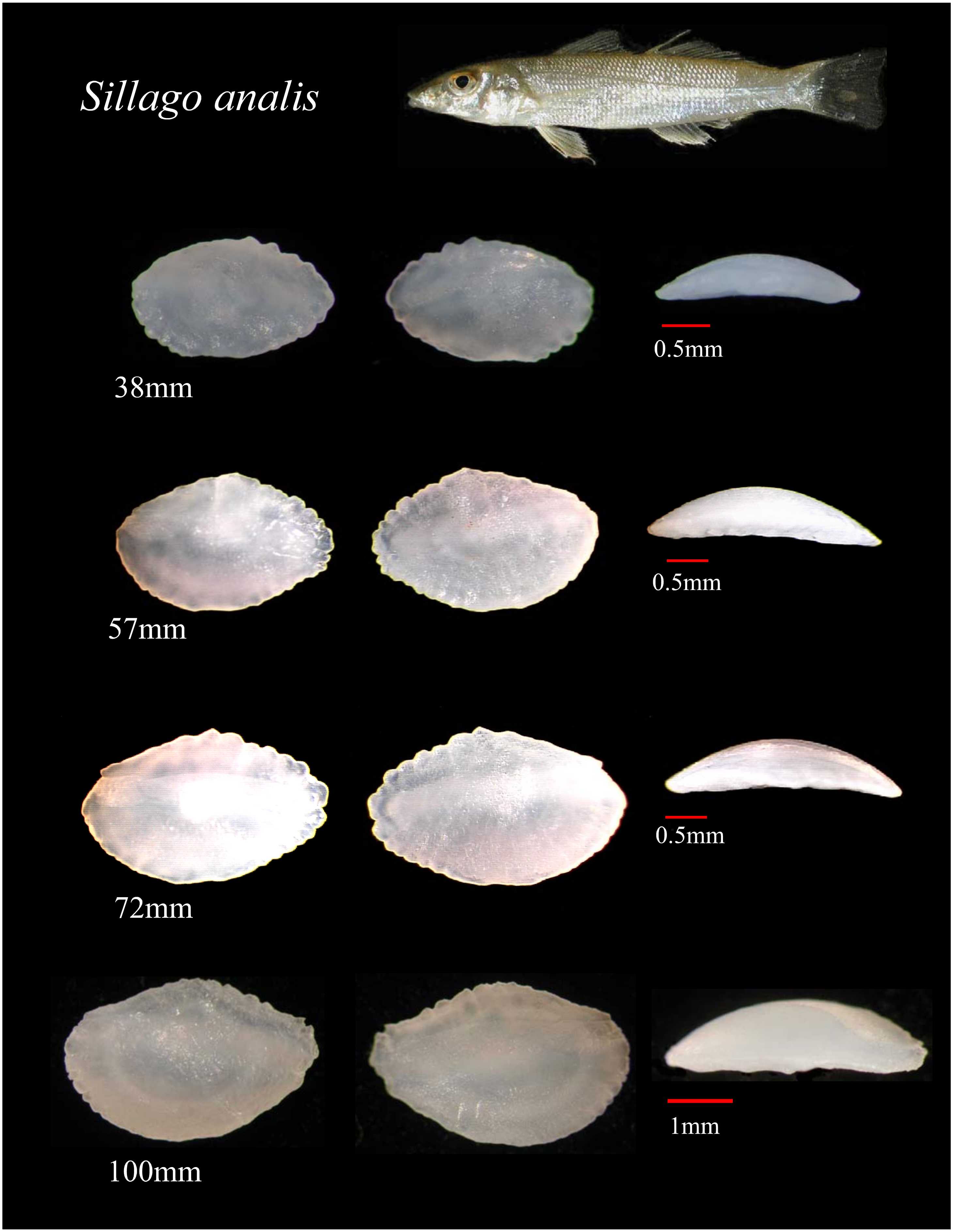
24mm

42mm

56mm


Secutor ruconius
13mm
0.5mm
24mm
0.5mm
34mm
0.5mm
41mm
0.5mm

Secutor insidiator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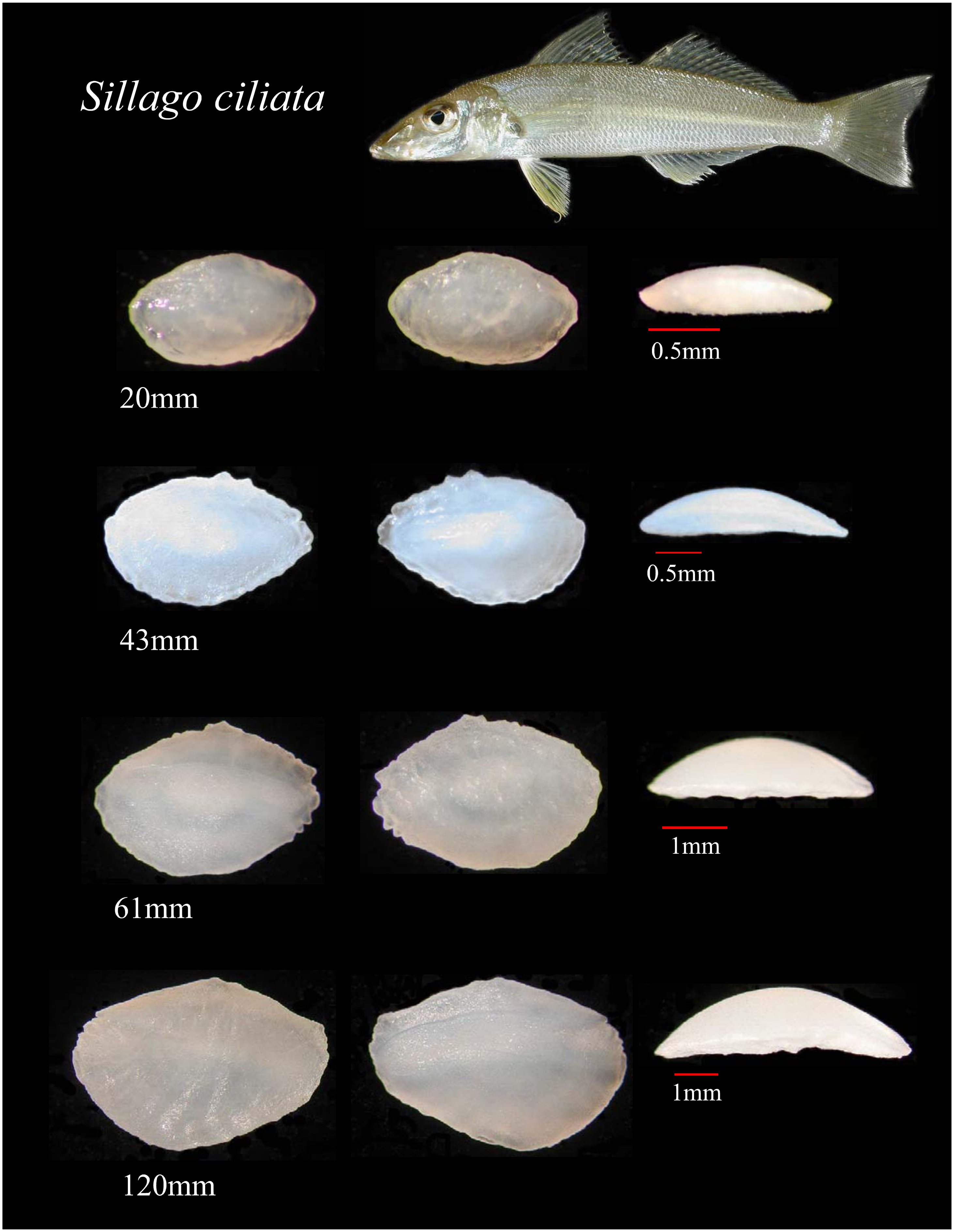
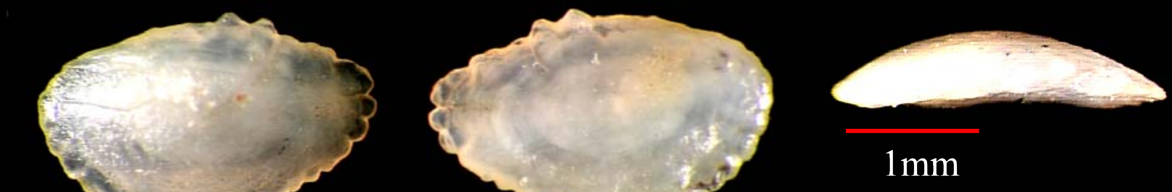
38mm
0.5mm
57mm
0.5mm
72mm
1mm
100mm

Sillago ciliata



Sillago maculata

25mm

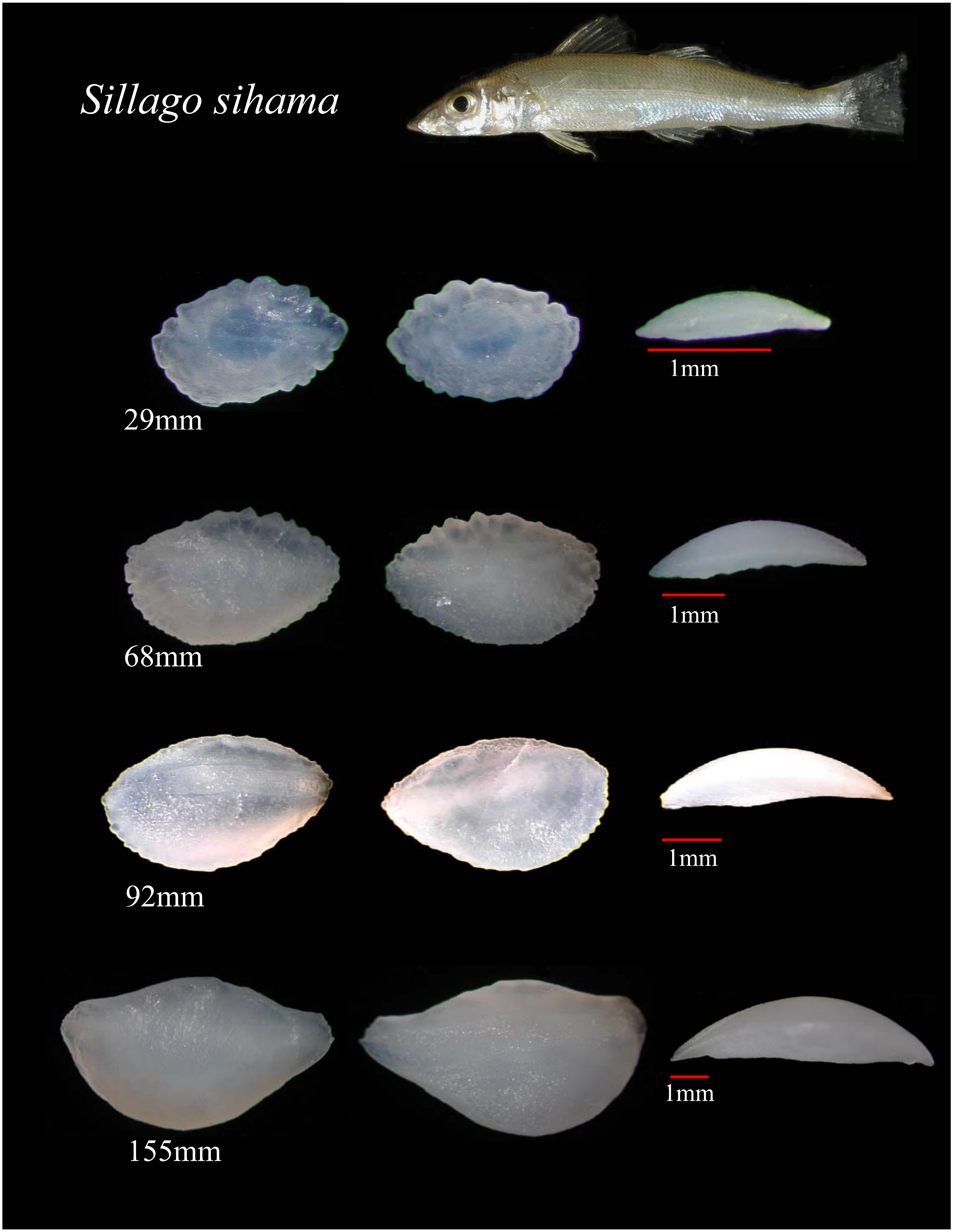


45mm

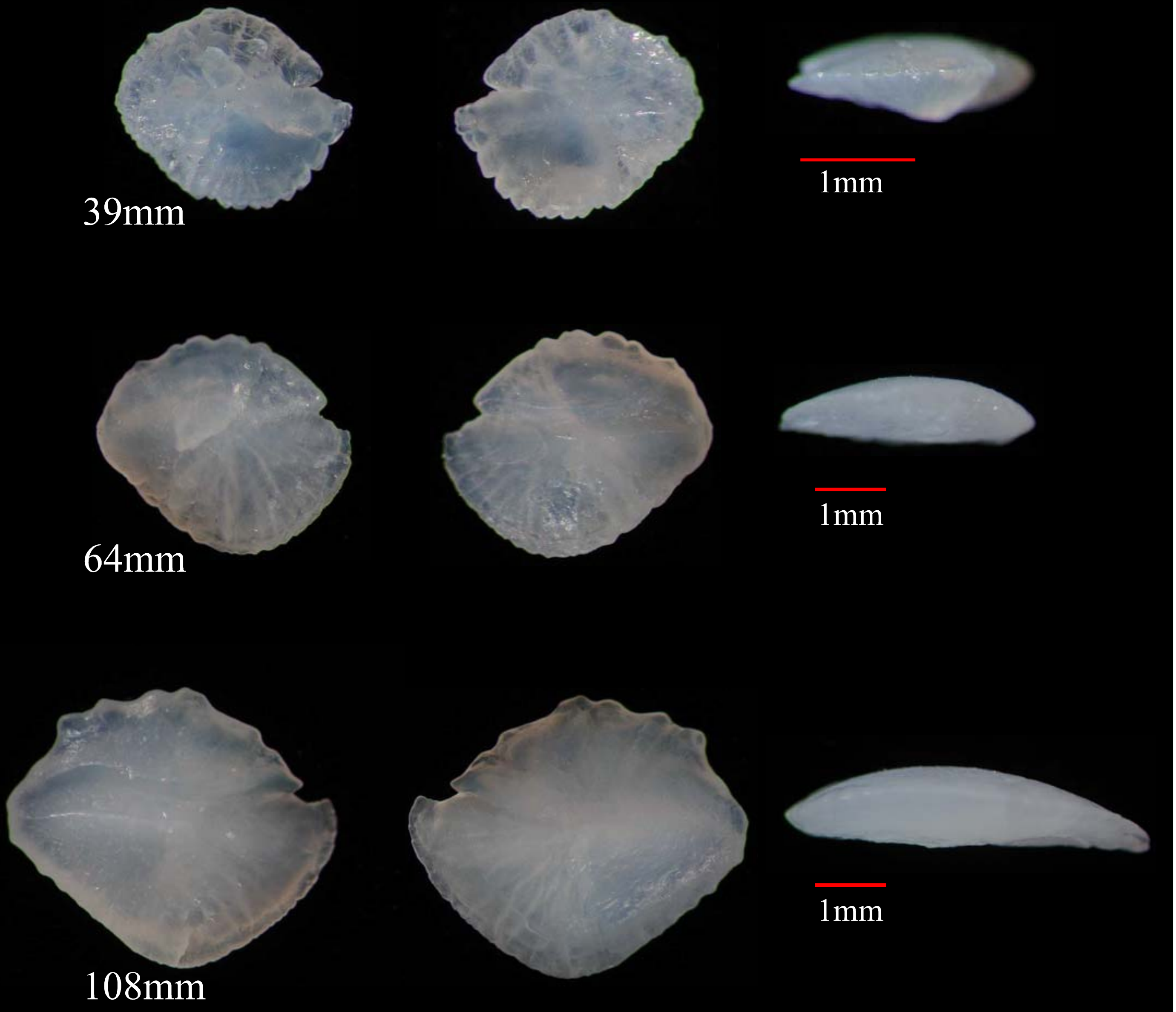
82mm

100mm

Sillago sihama



Ambassis nalua



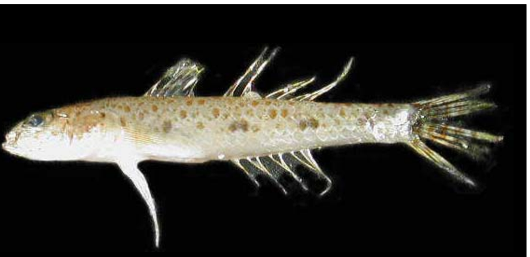
Ambassis telkara

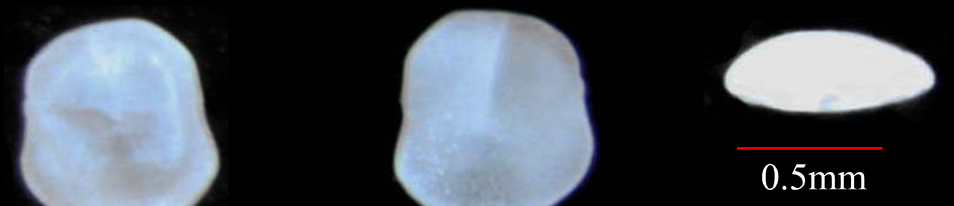
26mm

35mm

65mm

Acentrogobius viridipunctatus





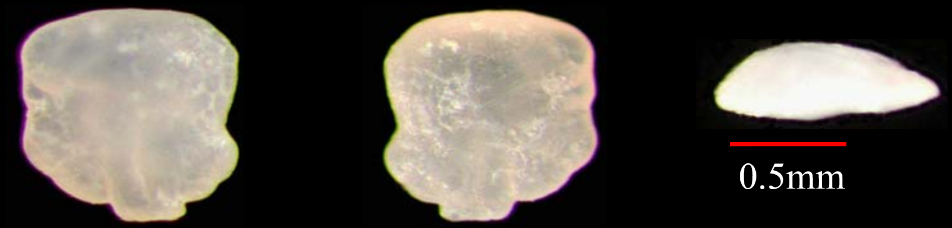
15mm

23mm

33mm

46mm

Psammogobius biocellatus



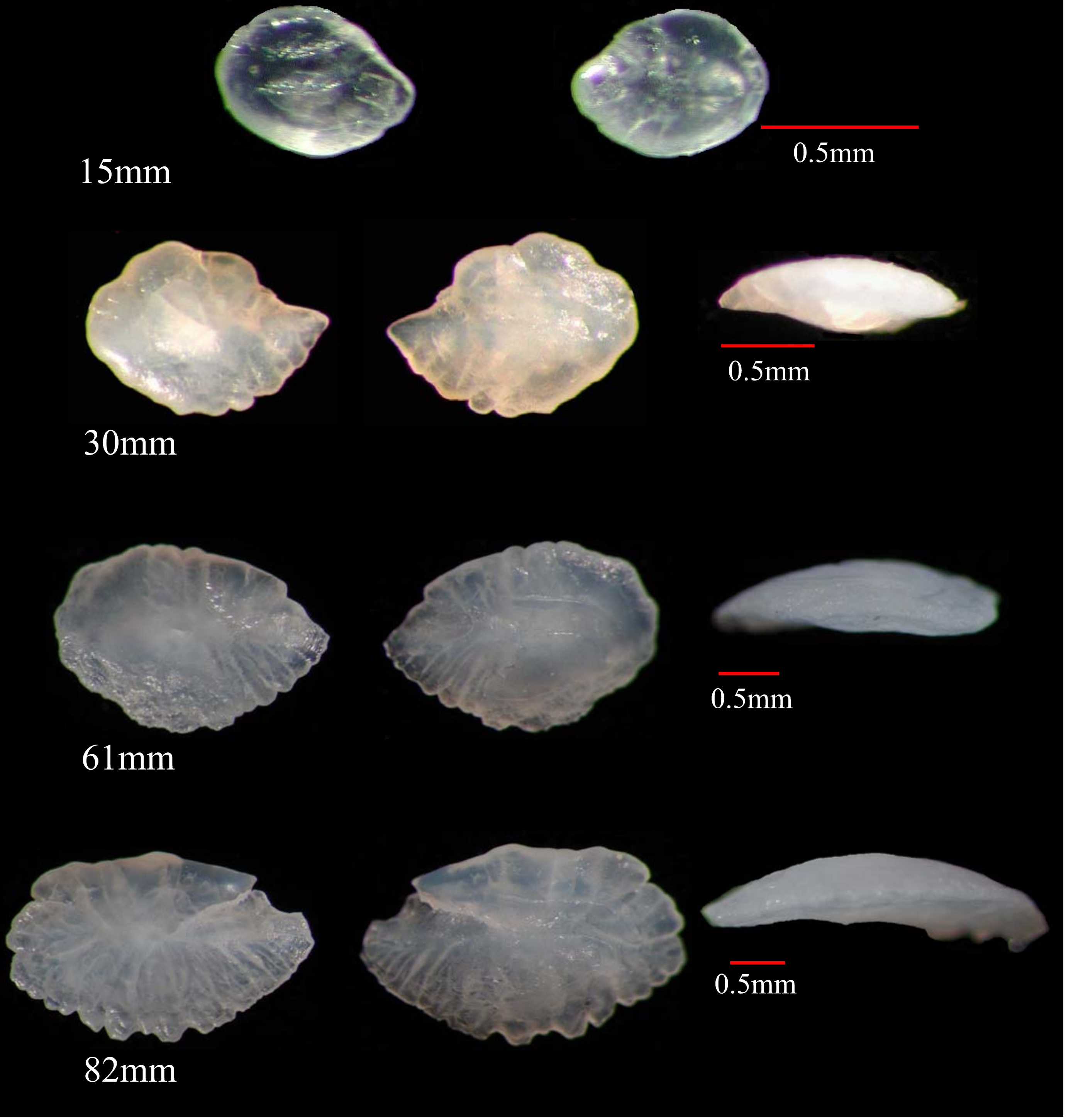
22mm

40mm

55mm

70mm

Gerres filamentosus

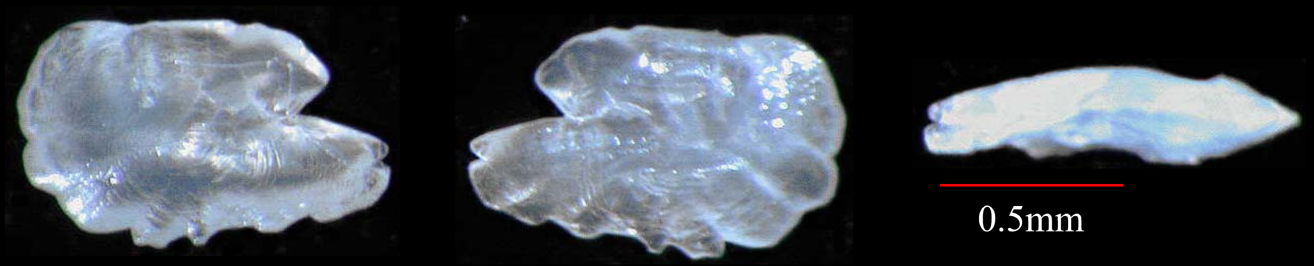


Herklotsicthys sp.

25mm

35mm

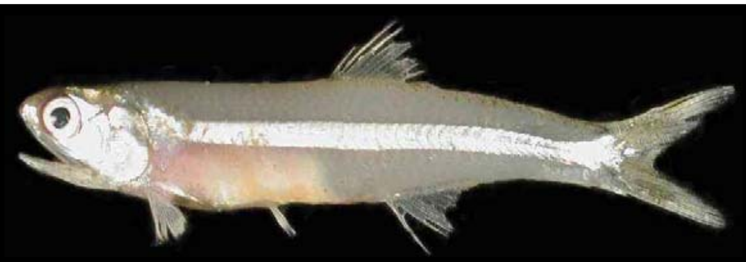
Sardinella sp.



45mm

72mm

Stolephorus sp.



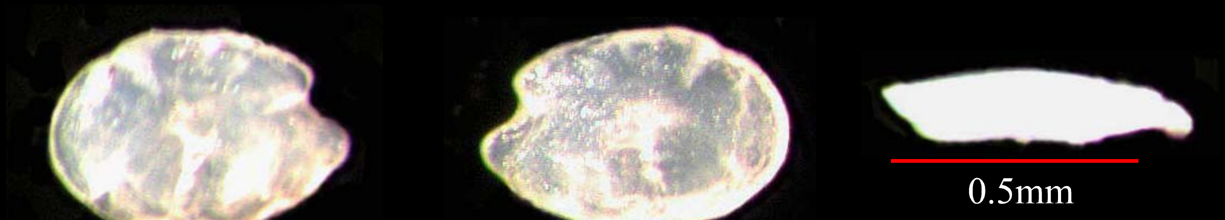
20mm

35mm

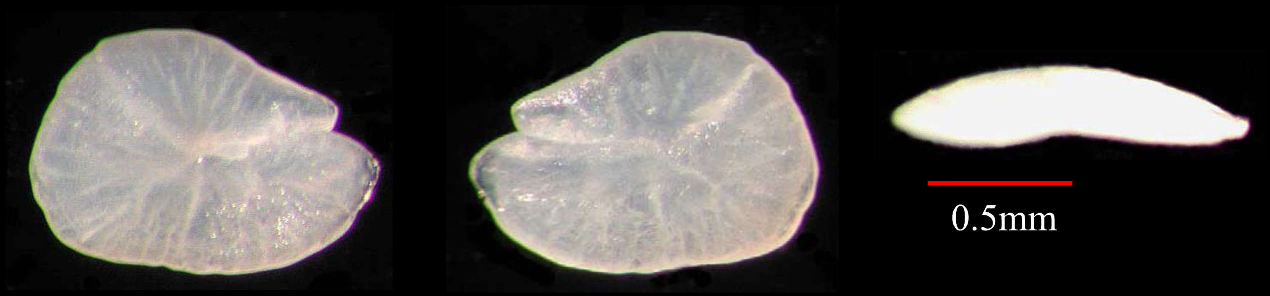
50mm

72mm

Hyporhamphus affinis



34mm



50mm

80mm

Hypoatherina temminckii

28mm

40mm

53mm

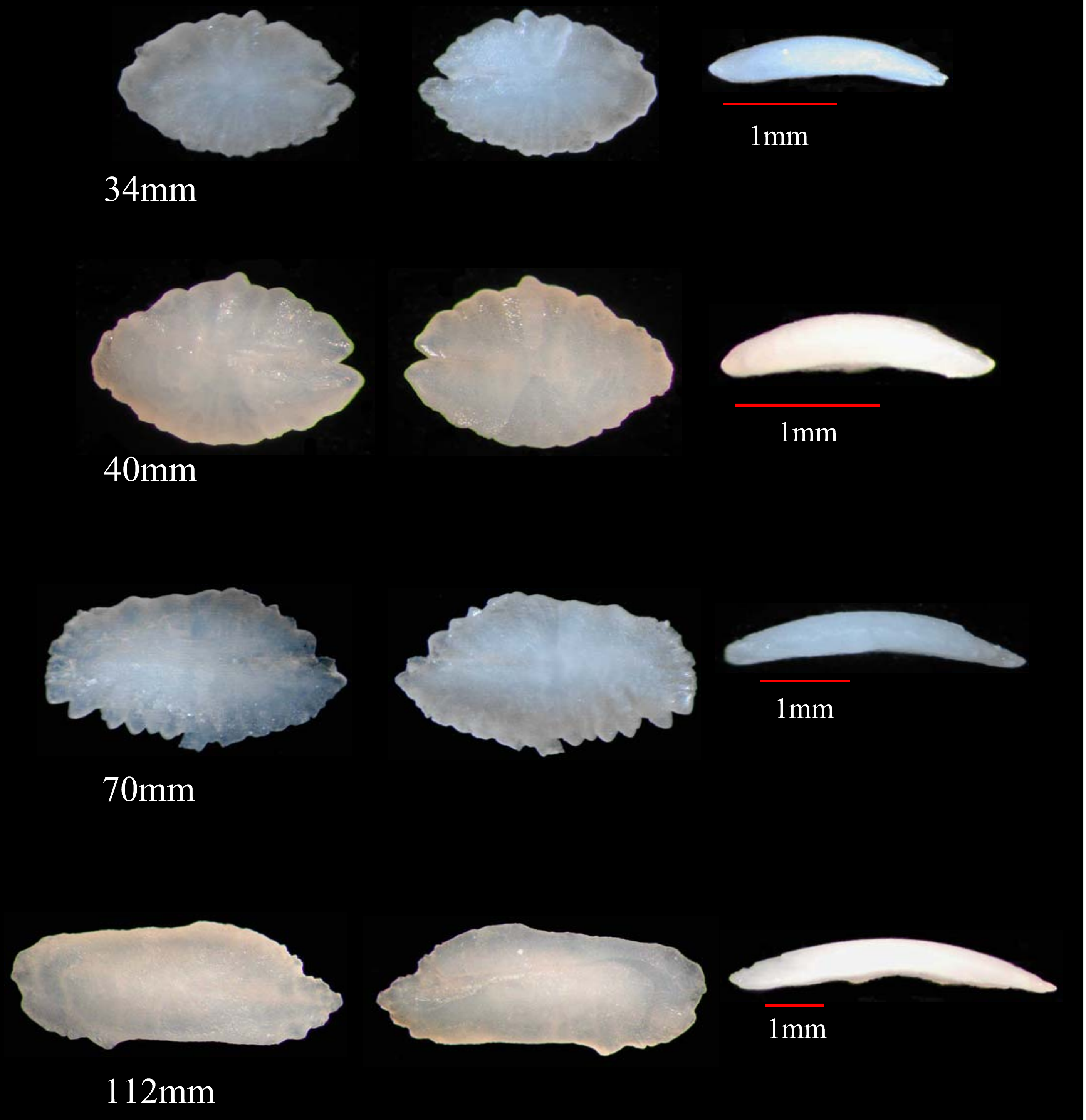
Mugil georgii

55mm

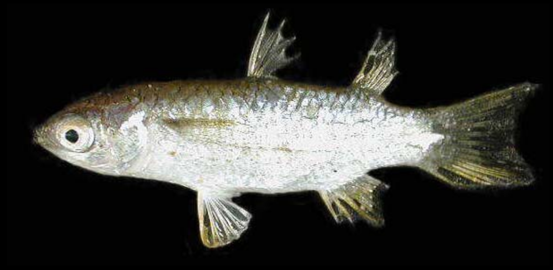
75mm

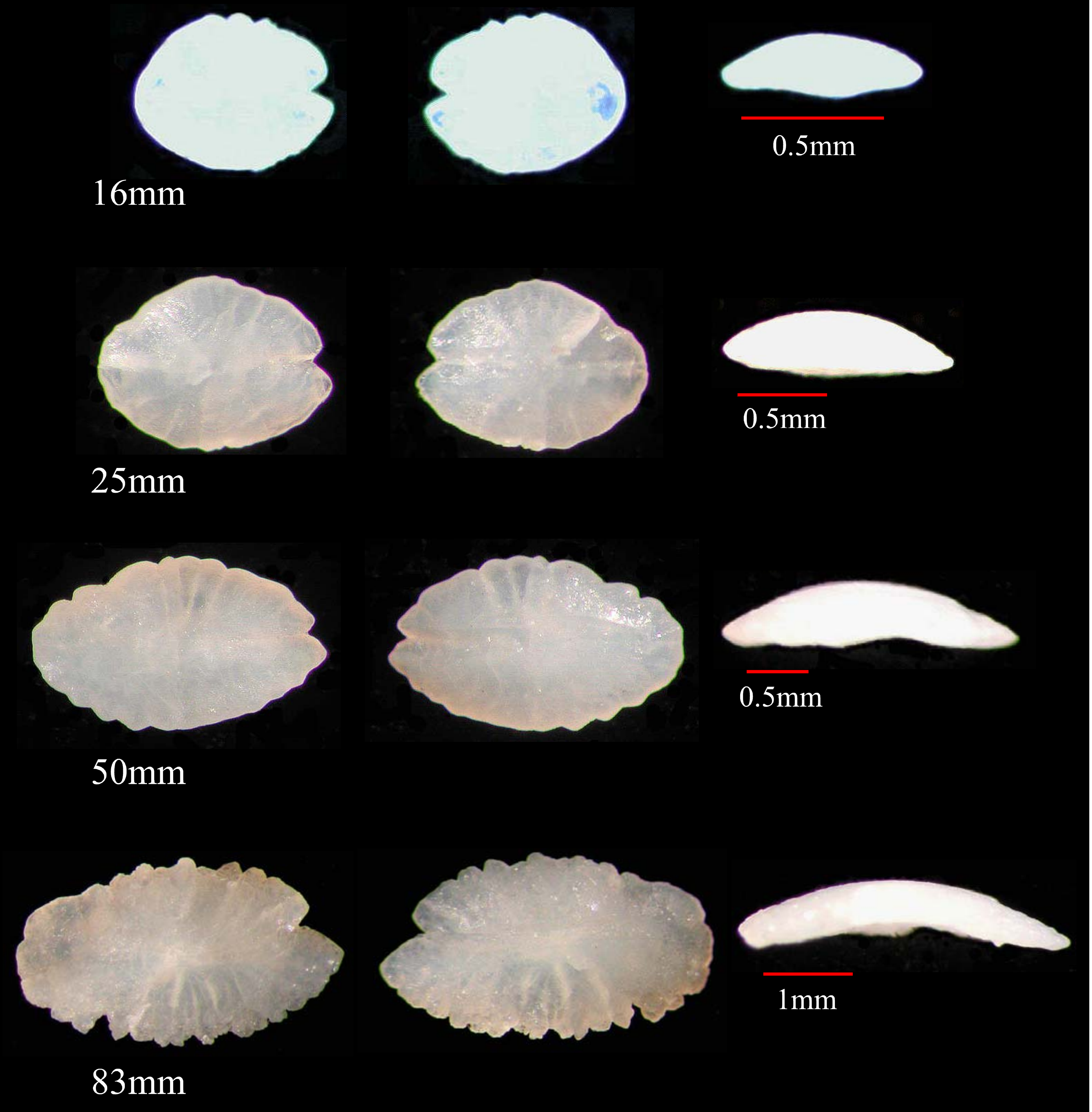
100mm

Liza subviridus



Liza vaigiensis





Valamugil buchanani

31mm

52mm

75mm

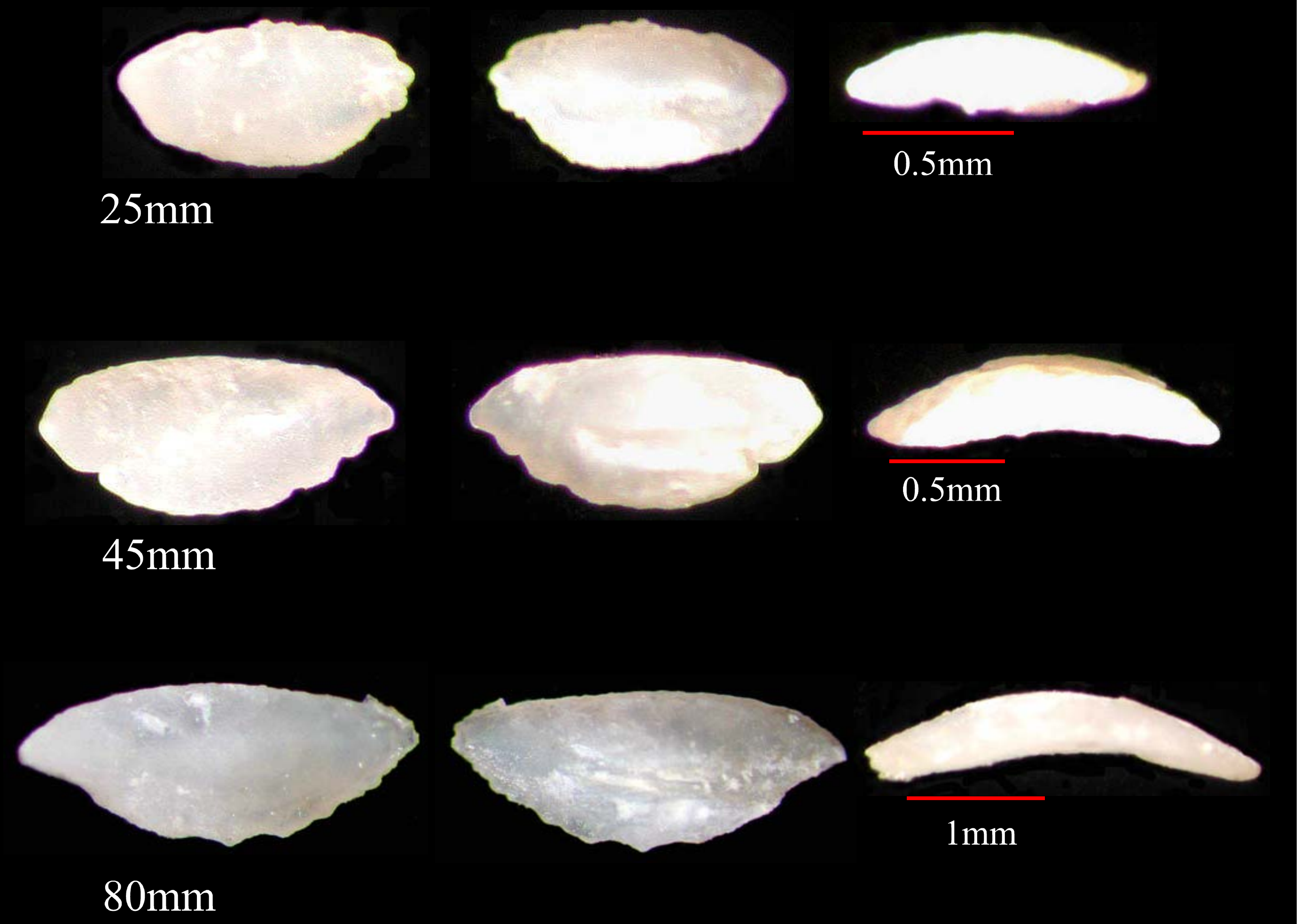
100mm

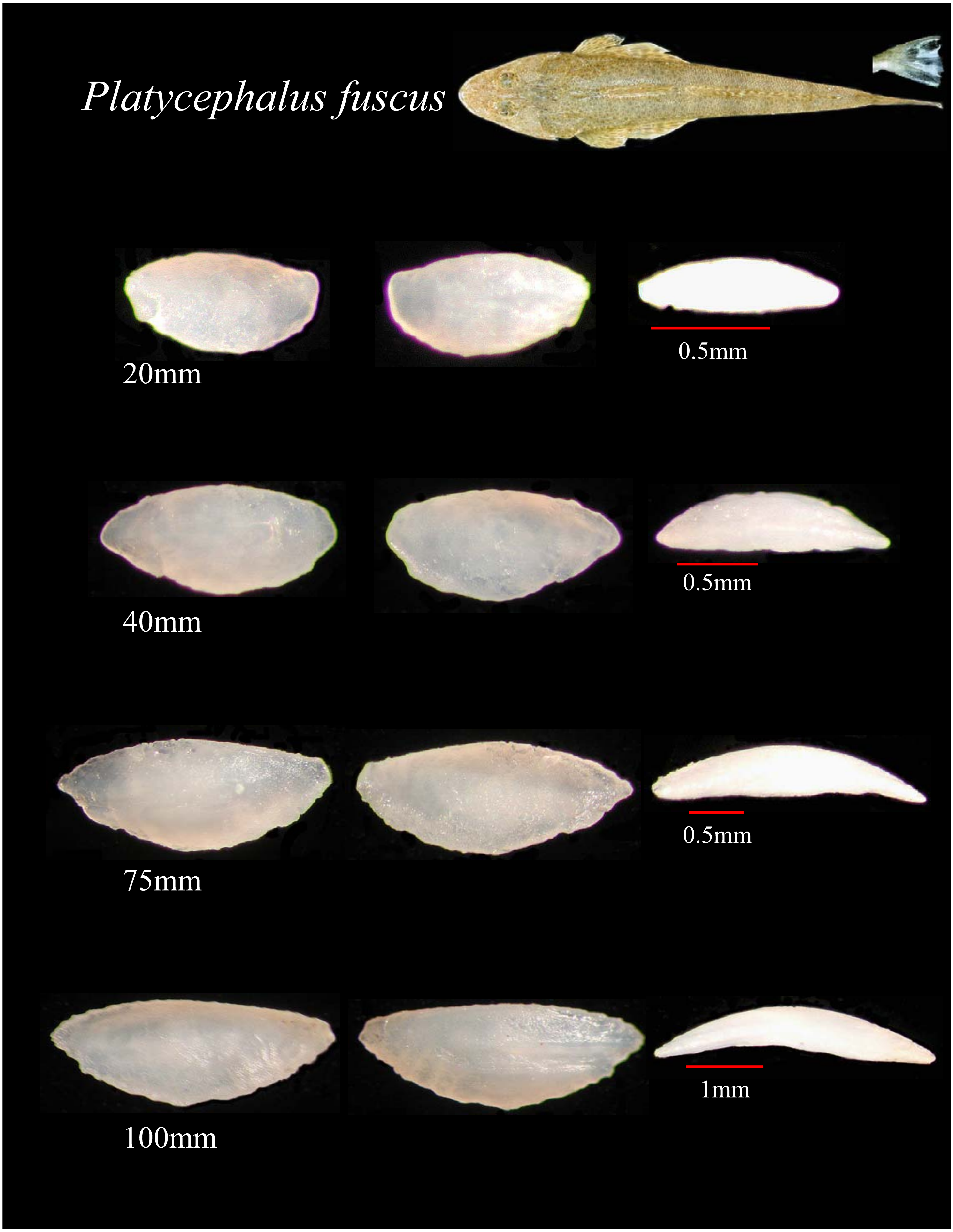
Valamugil cunnesius

77mm

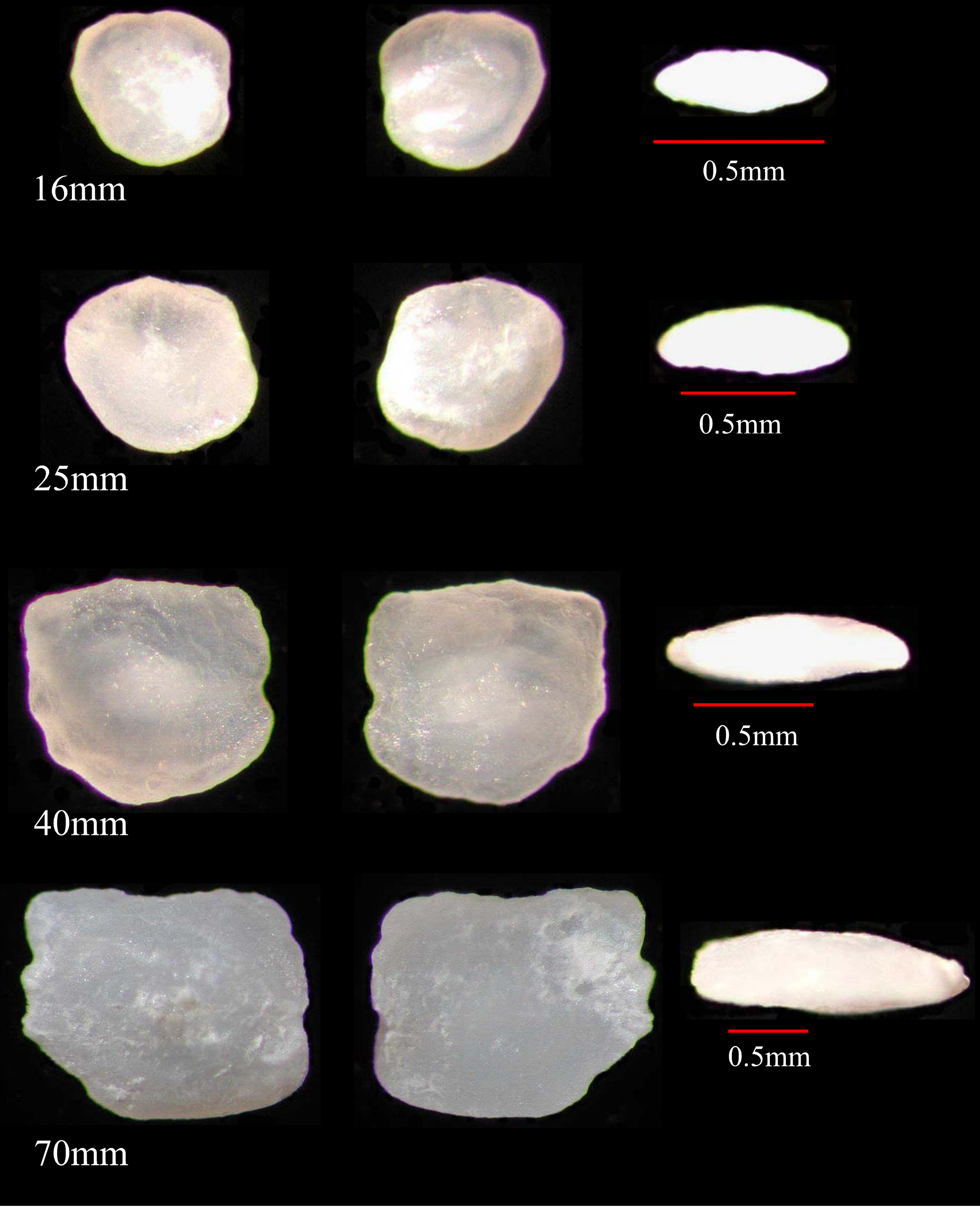
102mm

Platycephalus arenarius




Platycephalus fuscus
0.5mm
20mm
0.5mm
40mm
0.5mm
75mm
1mm
100mm

Pseudorhombus arsius



Appendix B: Results of individual chronographic tethering experiments.

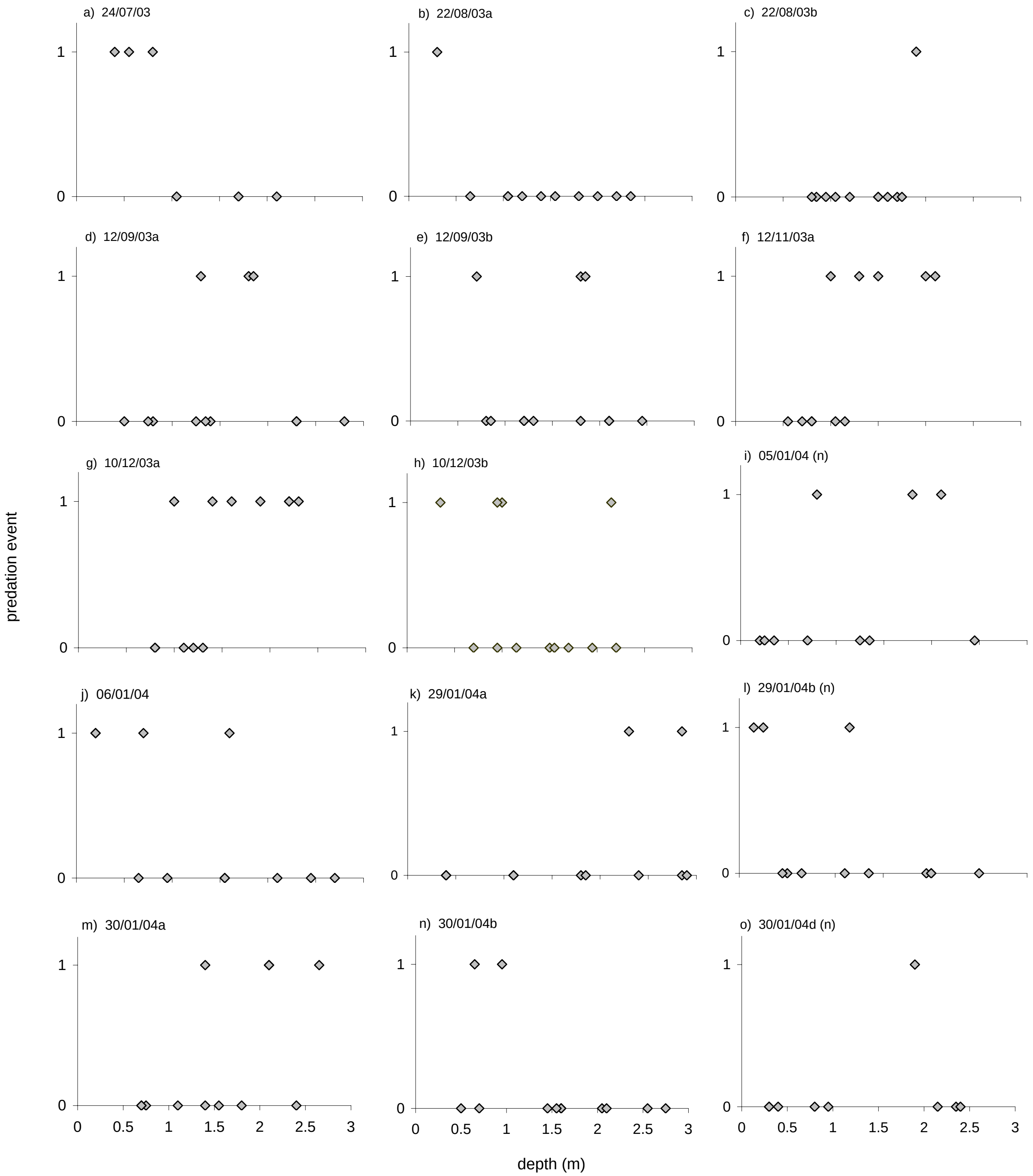

a) 24/07/03
b) 22/08/03a
c) 22/08/03b
d) 12/09/03a
e) 12/09/03b
f) 12/11/03a
g) 10/12/03a
h) 10/12/03b
i) 05/01/04 (n)
j) 06/01/04
k) 29/01/04a
l) 29/01/04b (n)
m) 30/01/04a
n) 30/01/04b
o) 30/01/04d (n)

Figure B1: Depth-related patterns in predation pressure on tethered fish prey (Chapter 6). 1 = predation event, 0 = no predation event. a) experimental trial in the Ross River, b) - o) Victoria Creek. The two trials in which no prey were taken are not shown (12/11/03b and 30/01/04c). (n) after date indicates night set.

Appendix C

Derivation of piscivore functional group size classes for inclusion in the piscivore relative importance model (Ch 7)

Taxa were divided into size classes that account for ontogenetic changes in the occurrence, number and type of fish prey in the diet. The minimum size of piscivory was the smallest sized individual of each taxon found to have consumed fish in this study (Ch. 3, Table 3.1), or reported in the literature, rounded down to the nearest 10 mm for those taxa which the minimum size was >20 mm, and to the nearest 5 mm for those with a minimum <20 mm (n = 1 taxon). For each genus the lowest value of minimum size of piscivory was used for all congeners. For example, the smallest *Sillago* spp. found with fish in the gut was a 37 mm *S. sihama* (Table 3.1), therefore, all *Sillago* spp. ≥30 mm were considered as potential piscivores in the piscivore relative importance model.

Ontogenetic size classes accounting for changes in the occurrence of fish in the diet were defined in chapter 3 using nMDS and cluster analysis. Similarly, piscivore taxa were divided into size classes based on ontogenetic changes in the number of fish prey per individual, using quantile regression (Scharf et al. 1998) and univariate CART analysis (De'ath & Fabricius 2000). See chapter 3 for examples of the use of these techniques. Quantile regressions were used to examine size-related changes in the number of fish prey in the diet. Taxa that showed a significant relationship for either the 50th (median) or 90th (maximum) quantile for either the number of total fish prey or number of new recruits were divided into size classes using univariate CART analysis with the number of fish prey per predator as the dependant variable, and the predator FL as the explanatory variable (Table C1). Size class divisions were also made when individuals above a particular size were no longer found to consume new recruits (e.g. *Platycephalus fuscus* >300 mm, *Pseudorhombus arsius* >160 mm; Fig. 3.6, Ch. 3).

Size class divisions based on changes in the number of fish prey were combined with those based on changes in the occurrence of fish in the diet to produce a simple set of size class divisions for each taxa that reflected each of the ontogenetic changes in the consumption of fish prey; size of first piscivory, ontogenetic changes in the occurrence of fish, number of total fish, number of new recruits and maximum size of consumption of new recruits. Only the abundant major piscivores had sufficient data on the consumption of fish prey to detect ontogenetic changes beyond the minimum size of piscivory (Table C1). As such, all other piscivore taxa (rarer major and all minor piscivores) were divided only at the minimum size of piscivory, defined as outlined above. The final size class divisions as used in the piscivore relative importance model and the parameter values used for each of these functional groups are presented in Appendix D.

Table C1: Summary of quantile regression and CART analysis used to determine piscivore size classes based on numbers of prey per predator. % occ. size class splits based on nMDS and cluster analysis, as per chapter 3.

	quantile regression slope ± 1SE[1]				size class splits (mm) – CART analysis (sample size)			
	total fish		**new recruits**				% occ. size class splits	**final combined**
Species	50th quantile	90th quantile	50th quantile	90th quantile	total fish	new recruits	(from Ch. 3)	**sizeclass**
Caranx ignobilis	ns - intercept = 5.7	0.037 ± 0.004***	-0.015 ± 0.004***	-0.039 ± 0.002***	<83 (8), >83(58)	<=117(11), >117(23)	-	<83, 83-117, >117
C. sexfasciatus	0.098 ± 0.018***	0.262 ± 0.013***	0.208 ± 0.022***	0.122 ± 0.023***	<148.5(30), >148.5(5)	<57.5 (8), >57.5 (5)	-	<58, 58-148, >148
Scomberoides commersonianus	insuff.	insuff.	insuff.	insuff.	-	-	<60, 60-300, >300	<60, 60-300, >300
S. lysan[2]	0.013 ± 0.002***	0.150 ± 0.010***	0.016 ± 0.003***	0.132 ± 0.006***	<204 (63), >204(18)	<185 (9), >185(15)	<55, 55-140, >140	<55, 55-140, >140
Pseudorhombus arsius	ns - intercept = 2.0	-0.006 ± 0.001***	ns - intercept = 1.0	-0.019 ± 0.004***	<115.5 (155), >115.5(16)	<37.5(8), 37.5-160(76), >160(0)	<30, 30-70, >70	<30, 30-70, 70-160, >160[3,4]
Platycephalus arenarius	ns - intercept = 1.0	ns - intercept = 2.0	ns - intercept = 1.0	ns - intercept = 1.4	-	-	<45, 45-85, >85	<45, 45-85, >85
P. fuscus[5]	0.002 ± <0.001***	0.011 ± 0.002***	ns - intercept = 1.0	ns - intercept = 3	<77(62), >77(93)	-	<50, 50-80, >80	<50, 50-80, 80-300, >300[3]
Psammogobius biocellatus	ns - intercept = 1.0	0.052 ± 0.010***	ns - intercept = 1.0	0.070 ± 0.004***	<69(67), >69(3)	<64(26), >64(2)	<40, 40-60, >60	<40, 40-65, >65

Notes:

[1] Slope significance: ***p<0.001; ns - not significant; insuff. - insufficient data for quantile regression

[2] *S. lysan* CART solutions were unstable, therefore, % occ. size classes were considered adequate

[3] *P. arsius* >160mm & *P. fuscus* >300mm did not consume new recruits

[4] only 2 individual *P. arsius* between 115.5 and 160mm, therefore 160mm split from # new recruits was chosen over 115.5 split from # total fish

[5] *P. fuscus* data used for *P. endrachtensis* in model.

Appendix D

Summary of parameter values calculated for use in the piscivore relative importance model, Chapter 7.

		parameter						
		occurrence of fish in diet			total # fish per predator		# new recruits	
Piscivore functional group	maj/min pisc	average	user defined	maximum	average	maximum	average	max
Ambassidae								
A. nalua >20mm	m	28	10	100	3.0	10	4.5	10
A. telkara >20mm	m	5.3	1	73	2.2	5	2.0	3
Apogonidae								
Apogonid	m	9.5	5	58	1.0	1	1.0	1
Belonidae								
Belonid ≥40mm	M	100	-	100	2.5	3	3.0	3
S. strongylura ≥40mm	M	62	-	80	1.9	7	2.2	6
T. crocodilus ≥40mm	M	74	-	90	2.0	5	2.0	4
T. gavialoides ≥40mm	M	93	-	93	1.6	4	1.0	1
Carangidae								
A. mate	M	100	-	100	91.6	250	22.0	22
C ign 20-83mm	M	88	-	100	2.4	4	1.0	1
C ign 84-117mm	M	88	-	100	13.4	31	13.7	23
C ign >117mm	M	88	-	100	8.6	42	2.6	11
C sex 20-57mm	M	78	-	100	3.2	14	3.4	14
C sex 58-148mm	M	78	-	100	10.0	33	20.0	33
C sex >148mm	M	78	-	100	25.4	61	27.0	47
G. speciosus ≥20mm	M	46	-	78	11.2	38	3.0	5
M. cordyla	M	100	-	100	650.0	650	0.0	0
S. commersonianus 20-59mm	m	29	10	50	1.0	1	1.0	1
S. commersonianus 60-300mm	M	88	-	100	2.0	5	1.0	1
S. commersonianus >300mm	M	88	-	100	4.4	20	1.0	1
S. lysan 20-54mm	m	37	25	82	3.0	15	2.0	2
S. lysan 55-140mm	M	64.3	-	100	2.3	10	2.8	7
S. lysan >140mm	M	93.5	-	100	10.1	39	11.2	36
S. tala ≥20mm	M	95	-	100	31.2	122	1.0	1
Trachinotus botla	M	67	-	67	4.0	7	1.0	1
Centropomidae								
L. calcarifer ≥20mm	M	67	-	100	6.0	16	1.0	1
Engrualidae								
Stolephorus sp. ≥40mm	m	22	2	40	1.0	1	1.0	1
T. hamiltonii ≥40mm	m	20	10	64.3	1.5	2	1.0	1
Gerreidae								
G. filamentosus >20mm	m	0.5	0.5	18.2	1.0	1	1.0	1
Gobiidae								
B. butis >20mm	m	5	5	33	6.0	6	6.0	6
P. biocellatus 20-39mm	M	33.5	-	66	1.0	1	1.0	1
P. biocellatus 40-65mm	M	67.7	-	100	1.4	10	1.4	4
P. biocellatus >65mm	M	76.2	-	100	2.3	6	5.0	5
Leiognathidae								
G. minuta >60mm	m	25	1	75	1.0	1	1.0	1
Leptobramidae								
L. mulleri	M	100	-	100	2.1	5	1.0	1
Lutjanidae								
L. fulviflamma ≥20mm	m	33	25	33	1.0	1	1.0	1
L. russellii ≥20mm	m	24	25	71	1.3	3	1.0	1
Lutjanus sp. ≥20mm	m	25	25	25	1.0	1	1.0	1
Paralicthyidae								
P. arsius 20-29mm	m	27	15	100	1.4	2	2.0	2
P. arsius 30-69mm	M	66	-	100	2.0	10	1.8	6
P. arsius 70-160mm	M	77	-	100	2.2	5	1.6	5
P. arsius >160mm	M	74	-	100	1.7	3	0.0	0
Platycephalidae								
P. arenarius 20-44mm	m	30.2	10	43	1.2	4	1.0	1
P. arenarius 45-85mm	M	58	-	100	1.4	3	1.3	2
P. arenarius >85mm	M	85	-	100	1.4	3	1.0	1
P. endrachtensis 20-49mm	M	100	-	100	1.0	1	1.4	3
P. endrachtensis 50-79mm	M	71.4	-	100	1.0	1	1.3	2
P. endrachtensis 80-300mm	M	57.9	-	100	2.7	6	1.2	2
P. endrachtensis >300mm	M	50	-	50	1.0	1	0.0	0
P. fuscus 20-49mm	m	17	5	80	1.4	4	1.4	3
P. fuscus 50-79mm	M	43.1	-	85.7	1.6	5	1.3	2
P. fuscus 80-300mm	M	78.2	-	94.6	2.8	30	1.7	4
P. fuscus >300mm	M	74	-	100	1.8	7	0.0	0
Suggrundus sp. ≥30mm	m	31	15	75	1.0	1	1.0	1
Polynemidae								
E. tetradactylum ≥20mm	M	74	-	83.3	1.0	1	1.0	1
Scomberidae								
Scomberomorus >4mm	M	94	-	100	1.5	5	1.5	3
Sillaginidae								
Sillago analis ≥30mm	m	2.2	1	60	1.0	1	1.0	1
Sillago ciliata ≥30mm	m	9	1	60	1.2	2	1.0	1
Sillago maculata ≥30mm	m	6.3	1	90	1.2	3	1.4	3
S. sihama ≥30mm	m	2.5	1	12	1.0	1	1.0	1
Sparidae								
A. australis ≥20mm	m	11	1	75	1.5	3	2.0	2
A. berda ≥20mm	m	11	1	44	1.5	3	2.0	2
Sphyraenidae								
S. barracuda ≥20mm	M	96	-	100	2.5	6	1.0	1
S. jello ≥20mm	M	100	-	100	1.8	3	1.5	2
S. obtusata ≥20mm	M	100	-	100	1.0	1	1.0	1
Sphyraena sp. ≥20mm	M	98	-	98	1.2	4	1.3	2
Synodontidae								
Saurida sp. ≥30mm	M	93	-	100	1.5	3	1.5	2
cf. S. gracilis ≥30mm	m	26	20	60	1.1	2	1.0	1
Terapontidae								
P. quadrilineatus ≥15mm	m	1.4	1	20	1.0	1	1.0	1
T. jarbua ≥30mm	m	9	1	100	1.3	2	1.4	2
Uranoscopidae								
I. lebek ≥20mm	M	67	-	83	2.2	7	1.3	2

Appendix E

Composition (abundance) of blocknet samples from Blacksoil marsh. For sampling details, see chapter 7.2.5

Table E1: Piscivores included in the piscivore relative importance model.

Piscivore functional group	**Major/minor**	**April 2003**	**August 2003**	**November 2003**	**April 2004**	**August 2004**	**November 2004**	**total**
Ambassidae								
Ambassis telkara ≥20mm	m	0	0	147	130	0	68	345
Belonidae								
Strongylura strongylura ≥40mm	M	40	6	1	6	1	0	54
Tylosurus crocodilus ≥40mm	M	0	0	2	8	0	0	10
T. gavialoides ≥40mm	M	0	0	0	6	0	1	7
Carangidae								
Scomberoides commersonianus 20-59mm	m	0	0	0	3	0	0	3
S. lysan 20-54mm	m	6	1	42	20	7	88	164
S. lysan 55-140mm	M	12	0	11	9	0	31	63
S. lysan >140mm	M	0	0	0	1	0	0	1
Engraulidae								
Stolephorus sp. ≥40mm	m	0	0	0	47	0	0	47
Gerredae								
Gerres filamentosus ≥20mm	m	33	14	683	527	157	52	1466
Gobiidae								
Psammogobius biocellatus 40-65mm	M	0	0	0	2	0	0	2
Lutjanidae								
Lutjanus fulviflamma ≥20mm	m	0	0	0	7	0	0	7
Paralicthyidae								
Pseudorhombus arsius 30-69mm	M	1	0	0	0	0	0	1
P. arsius 70-160mm	M	0	0	0	5	1	0	6
Platycephalidae								
Platycephalus endrachtensis 50-79mm	M	0	0	2	0	0	0	2
P. endrachtensis 80-300mm	M	0	0	2	4	0	0	6
P. fuscus 20-49mm	m	0	1	0	0	0	0	1
P. fuscus 50-79mm	M	0	0	0	1	0	0	1
P. fuscus >300mm	M	1	0	1	6	1	3	12
Sillaginidae								
Sillago analis ≥30mm	m	156	956	1024	390	324	377	3227
S. ciliata ≥30mm	m	144	345	480	38	94	9	1110
S. maculata ≥30mm	m	0	0	0	0	3	0	3
S. sihama ≥30mm	m	0	32	8	21	66	110	237
Sparidae								
Acanthopagrus australis ≥20mm	m	1	0	3	10	0	17	31
A. berda ≥20mm	m	3	0	3	9	5	19	39
Sphyraenidae								
Sphyraena barracuda ≥20mm	M	2	0	1	1	0	4	8
Terapontidae								
Terapon jarbua ≥30mm	m	62	16	7	74	10	12	181
total		461	1371	2417	1325	669	791	**7034**

Table E2: Likely piscivores not included in the model due to lack of data.

	(estimated)							
Atherinidae		0	0	0	3	0	0	3
Atherinomorus endrachtensis	m	0	0	105	157	0	3	265
Hypoatherina temminckii	m	0	0	95	322	0	209	626
Carcharhinidae								
Negaprion acutidens	M	0	0	0	0	0	1	1
Clupeidae		0	0	0	0	0	1146	1146
Sardinella sp.	m	0	0	2	0	0	0	2
Elopidae								
Elops hawaiiensis	M	0	0	0	0	0	1	1
Gerreidae								
Gerres abbreviatus	m	18	285	17	49	132	8	509
G. oyena ?	m	34	34	191	0	0	0	259
Gerres sp. A	m	0	0	4	0	0	0	4
Gerres sp. B	m	0	0	0	229	46	18	293
Leiognathidae								
Gazza minuta ≥60mm	m	0	0	0	2	0	2	4
Leiognathus equulus	m	0	0	1	64	0	2	67
Leiognathus spp.	m	0	0	6	35	0	255	296
Lutjanidae								
Lutjanus argentimaculatus ≥20mm	m	0	0	0	2	0	1	3
Pomadassidae								
Pomadassis argenteus	m	0	0	1	0	0	0	1
Sillaginidae								
Sillago spp. ≥30mm	m	0	0	0	0	0	12	12
Cephalopoda								
Squid	M	0	0	1	0	0	0	1
total other potential piscivores		52	319	423	860	178	1658	3490

Table E3: Other species caught at Blacksoil, but not piscivores or no data

Piscivore functional group	**Major/minor**	**April 2003**	**August 2003**	**November 2003**	**April 2004**	**August 2004**	**November 2004**	**total**
Ambassidae								
A. telkara <20mm	-	0	0	0	2	0	2	4
Chandidae								
Chanos chanos	-	5	0	0	7	0	0	12
Dasyatidae (Elasmobranchii - stingrays)								
Himantura uarnak	-	5	0	1	2	5	2	15
Pastinachus sephen	-	4	0	9	2	0	4	19
Echeneidae (remoras)								
Echeneis naucrates	-	0	0	0	0	0	2	2
Engraulidae								
Stolephorus sp. <40mm	-	0	0	0	33	0	0	33
Gerreidae								
Gerres filamentosus <20mm	-	0	0	20	4	0	12	36
Gobiidae								
Acentrogobius viridipunctatus	-	0	0	2	12	0	0	14
slender goby	-	0	0	0	0	0	1	1
Hemirhamphidae								
Arramphus sclerolepis	-	4	21	3	239	37	50	354
Hyporhamphus sp.	-	0	0	10	1	0	144	155
Leiognathidae								
Secutor ruconius	-	0	0	0	2	0	0	2
Mugilidae								
Liza subviridis	-	7	2	0	10	20	0	39
L. vaigiensis	-	66	61	96	361	143	50	777
Mugil cephalus	-	0	5	14	30	0	7	56
Valamugil sp.	-	1461	561	862	1854	1313	964	7015
Mugilidae	-	0	0	362	65	3	0	430
Portunidae (Crustacea)								
Scylla serrata	-	6	1	0	0	0	1	8
Rhinobatidae (Elasmobranchii - shovelnose shark)								
Aptychotremata sp.	-	0	0	1	2	0	0	3
Scatophagidae								
Selenotoca multifasciata	-	2	0	1	1	1	0	5
Siganidae								
Siganus lineatus	-	0	0	4	0	0	1	5
Sillaginidae								
S. analis <30mm	-	0	2	1	0	3	0	6
S. sihama <30mm	-	0	0	0	6	0	0	6
Sillago spp. <30mm	-	0	0	14	2	0	5	21
Terapontidae								
T. jabua <30mm	-	2	0	2	24	0	44	72
Teraponid juveniles	-	0	0	4	0	0	0	4
Tetraodontidae								
Arothron manilensis	-	0	0	18	0	0	0	18
Chelonodon patoca	-	0	0	0	1	0	19	20
Marilyna pleurosticta	-	0	4	0	0	4	0	8
Tetractenos hamiltoni	-	12	48	57	16	22	32	187
total other species		1574	705	1481	2676	1551	1340	9327
Grand total		**2087**	**2395**	**4321**	**4861**	**2398**	**3789**	**19851**

Appendix F

Digestion rate of fish and crustacean prey by common estuarine predators

Introduction

Experiments were run to determine the digestion rate of fish and crustacean prey by common estuarine predators. Understanding the rate at which dominant prey types are digested is useful for aiding the interpretation of the gut contents of field caught fish (Haywood 1995). If particular prey types are digested faster than others, then the faster-digested prey may be under-represented in gut content analyses, thus leading to biased estimates of the relative importance of various prey types in the diets of predators. Additionally, understanding the digestion rate of prey assists in determining periodicity in feeding by allowing estimation of the time of ingestion of partially digested prey items.

Methods

Predator collection and maintenance. Predatory fishes for use in the experiments were collected from shallow sandy banks in the mouth of the Ross River (146^{o}50'E, 19^{o}16'S) using a 6 mm mesh seine net on the 17th and 21st of November 2000. Captured fish were placed into two 70 L aerated holding tanks and transported to the laboratory. In the laboratory fish were held in small groups (1 – 10 individuals) in 70 L flow through plastic aquaria at 35 ppt salinity and 30 – 32.5 ^{o}C, and fed daily with dead fish and crustaceans captured from the Ross River mouth. One week prior to an experimental trial, the fish for that trial were transferred into separate 70 L aquaria, one or two fish per tank. Some fish were placed two-per-tank because some individuals did not feed as aggressively as others. Placing two such fish in a single tank seemed to illicit a competitive response, making them feed more quickly and thus making it easier to record the time of prey ingestion during experimental trials. Fish were starved for 48 hours prior to each experimental trial to ensure the gut was empty at the commencement of each experiment.

Prey collection. Prey were collected from the Breakwater Marina using a hand held dip net on the day of each experiment. For all experiments the prey used were *Ambassis telkara* (fish) and *Acetes sebogae australis* (Crustacea, Sergestidae). Prey were euthanased in and ice-seawater slurry. In the laboratory, a sufficient number of similar-sized prey for the experiment were blotted dry and individually weighed to the nearest 0.01 g. Individual prey (*Ambassis* or *Acetes*) were allocated randomly to treatment tanks.

Digestion experiments. Each experimental trial used similar sized individuals of one predator species and had two treatments, each allocated randomly to individual predators; 1) prey type (*Ambassis* [fish] or *Acetes* [crustacean]), and 2) digestion time (0:30, 1:00. 1:30, 2, 3, 4, 5, 6, or 8 hours). Not all treatments were used in all experiments if there were insufficient number of similar sized predators available for each trial, or if some individuals would not feed. Experiment 1 ran for only 6 hours, while for the remaining four trials, the 1:30 and 5:00 hour treatments were dropped from some experiments. In trial 5, using *Psammogobius biocellatus*, only 7 predators were available and thus only fish prey were used in this experiment.

Individual pre-weighed prey were dropped into each aquaria, 1 prey item per tank. The time of prey ingestion by the predator was recorded. Usually the prey was ingested within 30 seconds of feeding. Predators that did not feed within the 1st minute were checked every few minutes until the prey was eaten. Tanks with two predators were observed until one fed, and the other predator was then removed. Predators from each treatment were captured and euthanased in an ice-seawater slurry after the appropriate period of digestion.

In the laboratory predators were measured (total length [TL] to the nearest mm), weighed (to the nearest 0.01g) and the guts were dissected out and the prey examined under a dissecting microscope. Prey were allocated to a digestion-stage category. The digestion-stage categories were predetermined from the examination of the gut contents of field-caught fish (Table F1). Each prey item was blotted dry and weighed to the nearest 0.01 g to allow calculation of the proportion of the original prey weight remaining.

Table F1: Digestion stages of fish and shrimp-like crustacean prey, determined from the examination of the gut contents of >200 predatory fishes collected from shallow estuarine habitats.

digestion stage	description of prey remains
fish	
I	fish intact little or no sign of digestion, some skin and fin filament digestion
II	digestion obvious, head easily identifiable, eyes intact, skin and/or fins gone, flesh intact and attached to backbone
III	fins and skin gone, head just identifiable, viscera not attached, flesh falling apart
IV	otoliths encased, head not identifiable, flesh falling off back bone, lenses free
V	otoliths free, other bits present (lenses, b.bone fragments, clear tissue).
VI	free otoliths only
shrimp-like crustaceans	
I	intact, little or no sign of digestion, flesh clear as in life.
II	exoskeleton soft/crumpled, flesh opaque, otherwise intact.
III	carapace all/part gone, head mush - eyes/antennal scales OK, limbs part/all gone, abdomen intact, flesh falling apart
IV	eyes/antennal scales and 6th abdominal segment/uropods/telson identifiable, mushy flesh, exo. fragments, limbs gone
V	eyes and 6th/uro/tels, some tissue.
VI	eyes or uropods/telson only.

A total of 5 experimental trials were run, 3 using *Platycephalus fuscus*, 1 with *Pseudorhombus arsius*, and 1 with *Psammogobius biocellatus* as the predator (Table F2).

Table F2: Summary of the predators and prey used in the digestion rate experiments. Because only 7 individual *P. biocellatus* were available for experiment 5, only fish prey were used in this trial.

			mean TL	Prey weight (g ± 1SE)	
Experiment	predator species	n	(mm ±1SE)	*Ambassis*	*Acetes*
1	*Platycephalus fuscus*	16	96.4 ± 2.2	0.14 ± 0.006	0.12 ± 0.004
2	*Pseudorhombus arsius*	16	75.1 ± 1.5	0.13 ± 0.02	0.11 ± 0.02
3	*P. fuscus*	15	79.4 ± 2.1	0.04 ± 0.01	0.05 ± 0.01
4	*P. fuscus*	17	145.6 ± 7.9	0.15 ± 0.02	0.11 ± 0.02
5	*Psammogobius biocellatus*	7	66.1 ± 0.3	0.19 ± 0.004	-

Results and Discussion

Overall, digestion rates were similar regardless of predator species, prey type, or the size of the predator or prey (Fig. F1). Prey remains had been largely digested or passed into the intestine 6 – 8 hours after ingestion. Digestion rate appeared linear through time, with the only major deviation being the individual left to digest fish prey for 3 hours during flathead experiment 1 (Fig. F1a). This was the smallest individual and was fed the largest fish prey used in that trial, and was moved after feeding into another tank.

Given the results of these experiments, it seems reasonable to conclude that the predatory fishes examined during this study digest fish and crustacean prey at approximately the same rate. Assuming the experimental results are reflective of field digestion rates, and not confounded by factors such as recent feeding history or predator activity levels, the gut contents of field-sampled fish are likely to represent the last 6 – 8 hours of feeding.

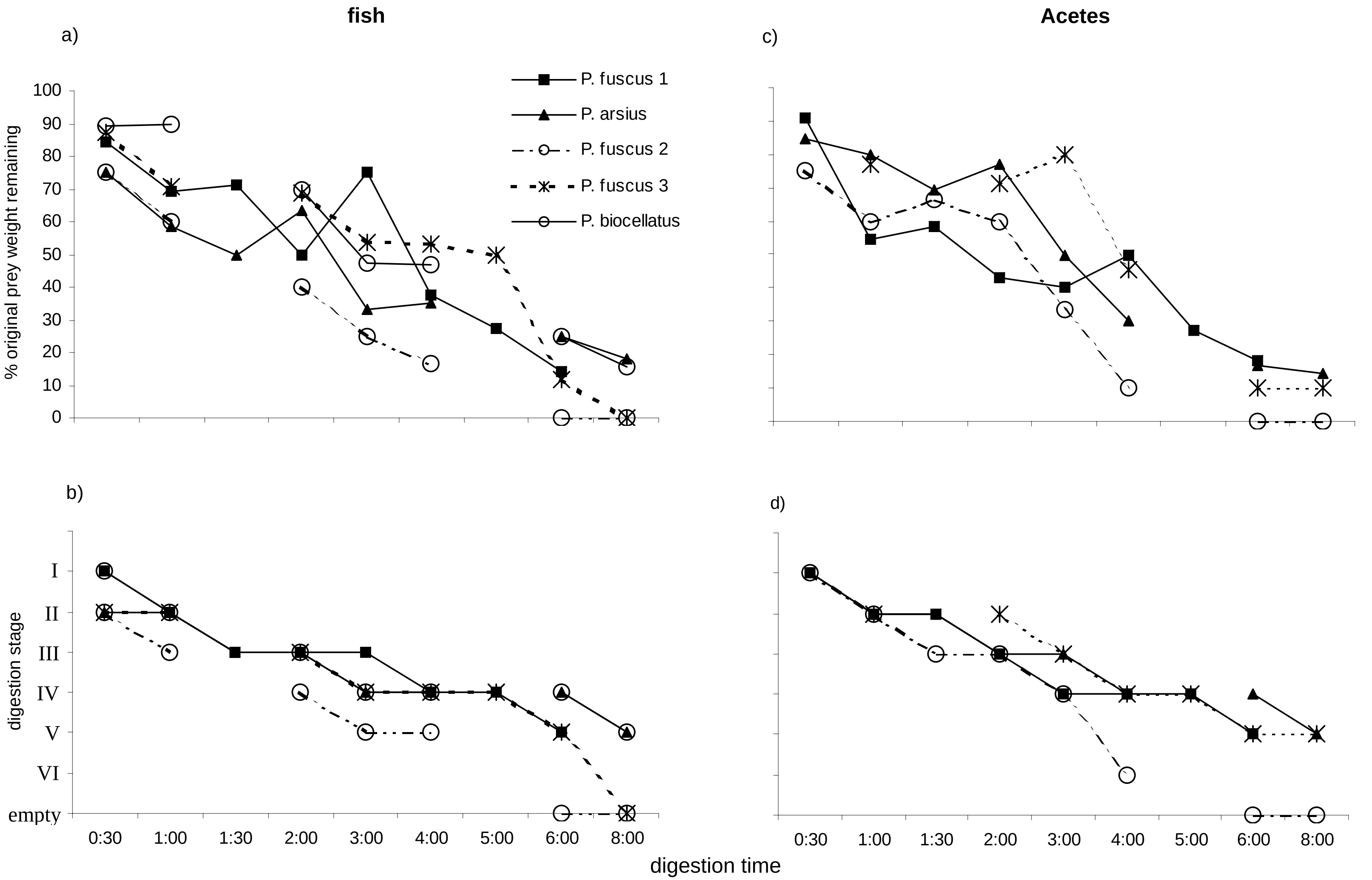


Figure F1: Digestion rate of a) & b) fish, and c) & d) crustacean prey by *Platycephalus fuscus, Pseudorhombus arsius* and *Psammogobius biocellatus*. All fish prey were *Ambassis telkara* (Ambassidae) and crustacean prey were *Acetes sebogae australis* (Sergestidae). a) & c) show the percentage of original prey weight remaining, while b) & d) show the digestion stage of the remaining prey, as per Table F1.

Appendix G

List of publications and conference presentations arising from this thesis

Papers

Baker R, Sheaves M (2005) Redefining the piscivore assemblage of shallow estuarine nursery habitats. Mar Ecol Prog Ser 291:197-213

Baker R, Sheaves M (in press) Visual surveys reveal high densities of large piscivores in shallow estuarine nurseries. Mar Ecol Prog Ser M6429

Baker R, Sheaves M (under revision) Minor piscivores: potentially major predators of new recruits to shallow tropical estuarine nurseries. (Rejected – Mar Ecol Prog Ser)

Baker R, Sheaves M (in prep) Do shallow tropical estuarine nurseries provide small fishes with a refuge from predation?

Conference papers

Baker R (2003) Piscivory and the value and functioning of shallow estuarine nurseries. Coastal CRC Conference, Coolangatta, September 2003.

Baker R, Sheaves M (2004) Defining the piscivore assemblage of shallow tropical estuarine nurseries. Australian Society for Fish Biology Conference, Adelaide, September 2004.

Baker R, Sheaves M (2005) Visual surveys reveal high densities of large piscivores in shallow estuarine nurseries. Australian Society for Fish Biology Conference, Darwin, July 2005.

Baker R, Sheaves M (2005) Do shallow tropical estuarine nurseries provide small fishes with a refuge from predation? Australian Marine Sciences Association Conference, Darwin, July 2005.

Baker R (2005) Juvenile fishes in estuarine nurseries: refugees or ravenous predators? Coastal CRC Conference, Coolangatta, September 2005.

Baker R, Sheaves M (2006) Against the flow: recruitment, predation and the contribution of coastal productivity to estuarine systems. Australian Marine Sciences Association Conference, Cairns, July 2006.

Baker R, Sheaves M (2006) Refugees or ravenous predators: detecting the impacts of predation in an inherently patchy environment. Australian Marine Sciences Association Conference, Cairns, July 2006.

Conference posters

Baker R (2003) Recruitment, predation and the trophic functioning of estuarine nursery grounds. Coastal CRC Conference, Coolangatta, September 2003.

Wilson J, Baker R, Sheaves M (2004) Trophic structure of a tropical estuarine fish assemblage in an intertidal bay. Australian Society for Fish Biology Conference, Adelaide, September 2004.

Baker R (2005) Small fish are important predators in shallow nursery habitats. Coastal CRC Conference, Coolangatta, September 2005.