

REVIEW

Are there really few piscivorous fishes in shallow estuarine habitats?

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ABSTRACT: Shallow estuarine habitats throughout the world are recognised as valuable nursery grounds for juvenile fishes. It is often suggested that this is due, at least in part, to the occurrence of low numbers of piscivorous fishes in these habitats. This idea is not confined to particular habitat types, but has been used in reference to a range of habitats, including both vegetated and unvegetated areas. I evaluate the proposition that there are few piscivorous fishes in shallow estuarine habitats, and suggest that the proposition is ill-defined, with little unequivocal supporting or contradictory evidence. To make any sense, the proposition must be evaluated relative to some other habitat, something often not addressed in previous studies. Additionally, including the full range of potentially piscivorous fishes is important if the role of predation is to be understood. Most studies have considered only large piscivorous fishes. This is unfortunate when the proposition logically relates to an advantage for small juvenile fishes. There is considerable evidence that, in addition to large piscivorous fishes, small juvenile fishes are extensively preyed upon both by juveniles of the large piscivorous species and by a range of other small species that include a large component of fish in their diets. In addition, many of the prey species may, themselves, switch opportunistically to piscivorous feeding. Not only are small piscivores numerous, but because of their size they are much more likely to access shallow waters than large piscivores. Even when the full range of piscivorous fishes are considered, it is not clear that the question of the abundance of piscivores in shallow waters should be the real focus of interest. Rather the crucial question is whether or not predator-induced mortality is reduced in shallow estuarine habitats.

KEY WORDS: Estuary · Fish · Piscivory · Tropical · Nursery ground

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INTRODUCTION

It is often argued that estuaries provide juvenile fish with a refuge from predation. This is often suggested to result from a reduction in the effectiveness of visual predators due to the turbid conditions occurring in many estuaries (Cyrus & Blaber 1992, Hecht & van der Lingen 1992, Maes et al. 1998) or because estuaries provide particular habitats in which there are relatively few predators. Although the idea of turbidity providing a refuge from predation is intuitive, the evi-

dence supporting reduced predator effectiveness due to turbid conditions is equivocal (R. W. Johnston et al. unpubl.). In fact some piscivorous fishes show little reduction in feeding under turbid conditions (Breitburg 1988, Chesney 1989, Greco & Targett 1996, Poling & Fuiman 1999), while others species may respond in contrasting ways. For example, Minello et al. (1987) found that high turbidity led to decreased predation by Atlantic croaker *Micropogonias undulates* on penaeid prawns *Penaeus aztecus*, but increased predation by southern flounder *Paralichthys lethostigma* on *P. aztecus*. These species-specific responses are not entirely unexpected because many piscine predators are not

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limited to visual prey detection but possess a range of sensory options. The case for a reduction in the efficiency of avian piscivores under turbid conditions seems less equivocal, given their highly visual nature (Safina & Burger 1985). It does seem likely that if predator efficiency is reduced by turbidity then reduced efficiency could lead to reduced predator carrying capacity and in turn to reduced predator abundance. This review will not deal with the effect of turbidity per se, beyond its potential as a factor that might lead to reduced predator abundance; rather I will concentrate on the proposition that there may be low numbers of piscivorous fishes in estuaries, particularly in shallow water habitats.

The idea that there may be few piscivorous fishes in shallow estuarine habitats has been reported often (Cain & Dean 1976, Shenker & Dean 1979, Blaber & Blaber 1980, Reis & Dean 1981, Boesch & Turner 1984, Rozas & Hackney 1984, Morton et al. 1987, Ronnback et al. 1999, Paterson & Whitfield 2000) from around the world (Table 1), and many more studies emphasise the value of shallow water habitats as refuges from predation (e.g. Miller et al. 1985, Russell & Garrett 1985, McIvor & Odum 1988, Robertson & Duke 1990, Paterson & Whitfield 1996, Vance et al. 1996, Lyse et al. 1998, Yozzo & Smith 1998). However, this view is by no means universal. For example, the results of nocturnal sampling of a New Jersey estuary cast doubt on the generality of the idea because substantial numbers of piscivorous fishes moved into shallow waters (<2 m) at night (Rountree & Able 1997). Additionally, there is an inherent conflict in the idea that shallow estuarine habitats provide both food and refuge for juvenile fish,

because most of the species using these habitats are themselves predatory to some extent (Kneib 1997). In this review I consider and discuss the evidence supporting the proposition that there are few piscivorous fishes in shallow estuarine habitats; I suggest that the proposition is ill-defined and that there is little unequivocal evidence to support or refute the idea. Additionally, I suggest that the crucial question is not one of predator abundance, but whether predator-induced mortality is reduced in these habitats compared to other habitats.

The literature I review relates to a diversity of shallow water, estuarine habitats such as salt marshes (Morton et al. 1987, Yozzo & Smith 1998), mangroves (Morton 1990), and unvegetated habitats (Ruiz et al. 1993). These habitats differ substantially in their complexity, and so, potentially, in the extent of refuge from predation they provide (Weinstein 1985, Everett & Ruiz 1993, Gotceitas & Fraser 1995, Sheaves 1996, Jordan et al. 1997, Rooker et al. 1998a). Despite this, I will consider the question of the use of shallow estuarine habitats by piscivorous fishes at a general level (disregarding habitat complexity or habitat type) because the idea that shallow waters have fewer piscivorous fishes has been suggested across a range of habitats, and because, in a number of studies, it is unclear exactly what type of shallow water habitat(s) were involved.

DEFINING THE PROPOSITION

Although reduced abundance of piscivorous fishes in shallow estuarine habitats is often reported, besides

Table 1. A selection of field studies that have discussed the abundance of piscivorous fishes in shallow waters, with information on depths considered and how information on deep waters was obtained

Source	System	Depth of sites	Information on deep water
Cain & Dean (1976)	South Carolina, USA	Intertidal	Other sources
Whitfield & Blaber (1978)	Lake St Lucia, South Africa	Shallow: unspecified Deep: apparently <2 m	Gill nets
Shenker & Dean (1979)	South Carolina, USA	Intertidal	Nil
Blaber & Blaber (1980)	Moreton Bay, Australia	Unclear; included subtidal	Other sources
Reis & Dean (1981)	South Carolina, USA	Intertidal	Nil
Rozas & Hackney (1984)	North Carolina, USA	Shallow: intertidal/Deep: subtidal	Gill nets
Rozas & Odum (1987)	Virginia, USA	Intertidal?	Nil
Morton et al. (1987)	Moreton Bay, Australia	Intertidal	Other studies
McIvor & Odum (1988)	Virginia, USA	Shallow: intertidal/Deep: subtidal	Electrofishing
Paterson & Whitfield (1996)	Kariega Estuary, South Africa	Intertidal	Nil
Rountree & Able (1997)	New Jersey, USA	Shallow: < 2 m	Nil
Ronnback et al. (1999)	Luzon, The Philippines	Intertidal	Nil
Paterson & Whitfield (2000)	Kariega Estuary South Africa	Shallow: intertidal and subtidal Deep: subtidal	All sites with gill nets

the work of Paterson & Whitfield (2000), evaluation of the proposition has rarely been the primary focus of study. Probably for this reason, many studies have simply noted a low number of predators (Cain & Dean 1976, Shenker & Dean 1979, Reis & Dean 1981, Morton et al. 1987) but made no comparisons with other habitats (Table 1). Clearly, to make any sense, the few piscivorous fishes proposition must be evaluated relative to some other habitat. A number of studies have done this, comparing catches in shallow estuarine habitats with those from nearby deeper waters (Rozas & Hackney 1984, Kneib 1987, McIvor & Odum 1988, Rountree & Able 1997, Paterson & Whitfield 2000), but most have not. Given that relatively few studies have addressed the question directly, the sampling biases apparent in many of the studies (Rountree & Able 1997) and the fact that a range of other issues cloud interpretation of many studies (see below), more extensive direct evaluation of the few piscivorous fishes proposition is clearly required.

As well as necessitating evaluation relative to other habitats, the proposition is only really meaningful if the abundance of piscivorous fishes is evaluated relative to the abundance of juvenile fishes within the habitat. This requires that both predators and their prey should be sampled with equal efficiency in both/all the habitats being compared. In a majority of situations this presents a substantial logistical problem, because most of the sampling tools currently available are either habitat specific (e.g. trap, block, flume, channel nets are limited to intertidal areas or at best to shallow subtidal areas) or unlikely to work with equal efficiency in all habitats (e.g. the efficiency of gill nets is likely to vary with water depth, current velocity and direction). It is hardly surprising, therefore, that few studies have been able to assess the proposition unambiguously.

Perhaps because the proposition has rarely been the primary focus of study, there are at least 2 other unresolved definitional problems: exactly what constitutes 'shallow water', and exactly which fishes should be considered as potential piscivores.

What constitutes 'shallow water'?

Although the few piscivorous fishes proposition refers to shallow waters, there seems to be no clear consensus about what actually constitutes shallow water. In some studies what is considered to constitute shallow water is unspecified; however, in many others shallow water refers to intertidal areas (Table 1). In contrast, Rountree & Able (1997) refer to waters less than 2 m deep when they suggest that predators may be more abundant in shallow waters than previously considered. This seems an incongruous definition

when 'shallow' in many other studies refers to intertidal waters. The difficulties with the lack of a consistent definition of shallow water are emphasised when you consider that one early study (Whitfield & Blaber 1978) appears to have defined their 'deep' sites as <2 m (Table 1), making them equivalent in depth to the shallow sites of Rountree & Able (1997).

How should 'piscivorous fish' be defined?

Few studies have explicitly delineated exactly what fishes should be considered piscivorous. However, many studies have made a tacit definition by confining their consideration to large or adult piscivores (Cain & Dean 1976, Blaber & Blaber 1980, Reis & Dean 1981, Morton et al. 1987, Ronnback et al. 1999, Paterson & Whitfield 2000). It is not intuitively obvious that the range of fish considered should be narrowed in this way. Indeed, doing so could lead to important components of the piscivore fauna being overlooked.

It seems sensible that any definition of a piscivorous fish should be relative to the size of the prey of interest, because susceptibility of prey to predation depends on predator-prey size relationships (Sogard 1997). The proposition under consideration relates to the value of shallow water estuarine habitats as nurseries for juvenile fishes. However, mortality is not distributed evenly over the juvenile period. Rather, mortality rates tend to decrease with increasing size (Peterson & Wroblewski 1984, Houde 1987). Indeed, predation is often targeted at smaller sized fish (Levin et al. 1997, Sogard 1997, Rooker et al. 1998a). This suggests that any advantage of a shallow water refuge would be most important to younger and smaller juveniles. It seems, therefore, that any consideration of the abundance of predators in shallow water needs to take into account the spectrum of predators likely to feed on smaller juvenile fishes. This leads to the question of predator-prey scaling (Sogard 1997).

Although many studies of predator-prey scaling have shown that large piscivorous fishes are capable of feeding on small prey (e.g. Popova 1978, Gleason & Bengtson 1996, Scharf et al. 1997, Buckel et al. 1998, Manderson et al. 1999, 2000, Hartman 2000), it is often small rather than large piscivores that preferentially target small prey fish (Rice et al. 1993). Additionally, a number of studies have shown that piscivores are able to consume prey that are large relative to the predator's size (Table 2). For example, summer flounder *Paralichthys dentatus* ingest winter flounder *Pseudopleuronectes americanus* up to 19% of their total length (Manderson et al. 2000) and striped sea robin *Prionotus evolans* feed on *Pseudopleuronectes americanus* up to 24% of their total length (Manderson et al. 1999), while

Table 2. Maximum lengths of prey fish able to be ingested by piscivorous fishes as a percentage of piscivore lengths

Species	% length	Source
<i>Aspius aspius</i>	31	Popova (1978)
<i>Esox lucius</i>	55	Popova (1978)
<i>Paralichthys dentatus</i>	19	Manderson et al. (2000)
<i>Perca fluviatilis</i>	45	Popova (1978)
<i>Prionotus evolans</i>	24	Manderson et al. (1999)
<i>Pomatomus saltatrix</i>	35 (whole ingestion)	Scharf et al. (1997)
<i>Pomatomus saltatrix</i>	60 (in pieces)	Buckel et al. (1999b)
<i>Silurus glanis</i>	41	Popova (1978)
<i>Stizostedion lucioperca</i>	43	Popova (1978)
<i>Stizostedion vitreum</i>	51	Knight et al. (1984)

young-of-the-year bluefish *Pomatomus saltatrix* can consume prey up to 35% of their length by ingesting them whole (Scharf et al. 1997) and up to 60% of their length by biting their prey into pieces (Buckel et al. 1999b). In addition, predation on large prey can be quite successful. Young striped bass *Morone saxatilis* can capture prey fish with up to 50% attack success at prey:predator size ratios as great as 0.3 (Hartman 2000). Moreover, many piscivorous fishes have been shown to undertake substantial piscivory at a very early stage. For example, the barracuda *Sphyræna barracuda* is almost exclusively piscivorous from lengths as small as 20 mm (Blaber 1982), and age 0 *P. saltatrix* (99%) and weakfish *Cynoscion regalis* (88%) derive most of their nutrition from fish prey (Hartman & Brandt 1995). Thus, it seems unreasonable to limit consideration to large piscivores. For instance, if we assume that many predators are capable of feeding on prey up to 39% of their length (the mean of maximum prey ratios in Table 2), then small juvenile fish of 15 to 25 mm would be vulnerable to predators of 38 to 64 mm, fish that would not usually be considered as 'large predators'.

Including small individuals of large piscivorous species is important because small piscivores can occur in high densities in shallow waters. For instance, the flathead *Platycephalus fuscus* is a specialist, shallow water, estuarine piscivore (Sheaves & Molony 2000), endemic to eastern Australia. Daytime seine netting (12 mm mesh) from shallow (<1 m) sandy habitats of 10 estuaries in tropical Australia over 2 yr captured medium to large *P. fuscus* (150 to 680 mm total length) at maximum average densities of 0.0029 ± 0.0011 (SE) m^{-2} , but small juvenile *P. fuscus* (35 to 85 mm total length) at average densities up to 0.36 ± 0.10 (SE) m^{-2} (author's unpubl. data). Similarly, young-of-the-year *Pomatomus saltatrix* are both piscivorous (Juanes et al. 1994, Buckel et al. 1999a,b) and highly abundant in estuaries of the Mid-Atlantic Bight (Rountree & Able

1997, Buckel et al. 1999a). Young-of-the-year *P. saltatrix* are important piscivores, to the extent that they play a major role in regulating abundances of young-of-the-year *Morone saxatilis* (Juanes et al. 1993, Buckel et al. 1999a) and other species (Juanes et al. 1993). Moreover, young-of-the-year *P. saltatrix* are among the most abundant fishes in shallow marsh creek habitats (Rountree & Able 1992, 1997) and concentrate most of their feeding during daylight hours, the time when they are most abundant in shallow, near-shore waters (Buckel & Conover 1997). Thus even without considering 'large piscivorous fishes' it seems that

the proposition is unlikely to be valid for many shallow water habitats in the Mid-Atlantic Bight. Small predators are important elsewhere also. For example, predation by juvenile bass *Dicentrarchus labrax* on younger conspecifics is so intense that the presence of a strong year class leads to very low recruitment of following year classes to the adult population, even under favourable environmental conditions (Henderson & Corps 1997).

As well as occurring in high densities, juveniles of predatory species have the potential to exert considerable predation pressure on prey stocks. Because of high early mortality rates, juveniles are likely to be much more abundant than their larger conspecifics (Peterson & Wroblewski 1984, Houde 1987). Consequently, because there are large numbers of juveniles relative to adults, and juveniles have a much greater requirement for food per unit body weight, the consumption curve of a fish population is shifted towards juveniles (Yañez-Arancibia et al. 1994). Thus the juvenile portion of the fish population consumes more prey than the adult component (Yañez-Arancibia et al. 1994) leading to the likelihood that juvenile predators could have a greater impact on prey species than their larger conspecifics. It also makes sense that small individuals are exactly those likely to make use of shallow waters, because their mobility should be less limited by shallow water than large predators.

Including small piscivorous fishes can make a difference to the perception of the abundance of piscivorous fishes in shallow waters. For example, Blaber & Blaber (1980) reported few 'large piscivorous fishes' from their shallow water sampling sites in Moreton Bay, Australia. However, their Table II shows that piscivorous fish were not absent from shallow waters. Teleosts contributed substantially to the diets (>40 to 92% frequency of occurrence) of 5 of the 25 species captured in shallow water: *Alepes djedaba* and *Scomberoides tol* (Carangidae), *Pomatomus saltator* (Pomatomidae),

Sphyraena obtusata (Sphyraenidae) and *Tylosurus macleayanus* (Belontiidae), at least 2 of which (*A. djedaba* and *S. obtusata*) were abundant in shallow waters. In addition, juveniles of 2 species of carangids, *Caranx ignobilis* and *C. sexfasciatus*, were captured in low numbers. These are known to be primarily piscivorous (Blaber & Cyrus 1983) and, due to their mobile nature, may well have been poorly represented in the samples of Blaber & Blaber (1980) (see below).

Not only does including smaller piscivorous fishes entail considering small individuals of the large piscivorous species, it also necessitates considering a range of other species that may contribute substantially to predation on small juvenile fishes. For example, glassfishes *Ambassis* spp. are small (most species <10 cm standard length), abundant components of fish faunas over much of the Indo-west Pacific (Martin & Blaber 1983, Allen & Burgess 1990). Martin & Blaber (1983) found that small juvenile and larval fish contributed between 12 and 31% of the energy acquired by 3 species of *Ambassis* in 6 South African estuaries. Given that members of the genus *Ambassis* are often among the most dominant components of catches from Indo-west Pacific estuaries (Robertson & Duke 1990), they have the potential to contribute substantially to predation on small juvenile fishes. Similarly, pinfish *Lagodon rhomboides*, a small sparid fish, is the dominant species in seagrass meadows of the Aransas Estuary, southern USA (Rooker et al. 1998b), and has been shown experimentally to be a voracious predator on young, juvenile red drum *Sciaenops ocellatus* (Fuiman 1994). As a consequence, *L. rhomboides* has the capacity to cause massive mortality of young, juvenile red drum (Rooker et al. 1998a,b).

The perception of piscivore abundance and thus predation pressure may also be considerably altered if small individuals of species not normally considered as piscivores are included. For example, while investigating the predators of penaeid shrimps, Haywood et al. (1998) sampled fish from 2 intertidal estuarine seagrass beds in tropical Australia using gill nets, beam trawls, seine nets and rotenone. They reported the diets of 40 species of fish for which the stomachs of 10 or more individuals contained food. Although the study was not focussed primarily on piscivory, the range of sampling gears provides a sample of fish over a broad size range, making it useful for the purposes of illustration. Of the 24 species that had fed on teleost prey (Table 3) only 9 occurred at lengths greater than 210 mm. Even though the remaining 15 species had consumed teleost prey, it is unlikely they would be considered to be large piscivores. For example, few fish of less than 210 mm are likely to be retained in 100 mm mesh gill net such as that employed by Paterson & Whitfield (2000) to sample large piscivores (one of the few studies to directly address the proposition that there are few piscivorous

fishes in shallow estuarine habitats). Even though the 15 species from Haywood et al. (1998) that had consumed fish included no species where more than 20% of individuals had fed on teleost prey, the presence of fish in their diet indicates that a substantial number of fish that could contribute to shallow water piscivory would not be included if only large piscivores were considered. Moreover, other studies in tropical Australian estuaries have reported much higher percentages of fish in the diets of some of the species in similar size ranges to those captured by Haywood et al. (1998). For example, 58% of *Apogon ruppelli* and 39% of *Ambassis nalu* from the Embley Estuary, Australia, had consumed piscine prey (Salini et al. 1990), while 20% of *Thryssa hamiltoni* from the Norman River, Australia, had ingested fish (Salini et al. 1998). Additionally, in the samples of Haywood et al. (1998), 3 of the species with more than 40% occurrence of teleost prey, *Scomberoides commersonianus*, *Cymbacephalus nematophthalmus* and *Platycephalus indicus*, were caught down to sizes (Table 3) at which many individuals would not have been retained had a 100 mm gill net been used, suggesting that even small, primary piscivores would not have been recorded as present.

Even when the whole spectrum of piscivorous fishes (both large and small, adult and juvenile) is considered, there is still one group of potential piscivores to be considered: those members of the fish assemblage that are not normally piscivorous but can switch to feeding on juvenile fish when they are abundant. Prey switching has been documented many times in a range of different systems (e.g. Stergiou & Fourtouni 1991, Aarnio et al. 1996, Olson 1996, Dawe et al. 1998, Merigoux & Ponton 1998, Manderson et al. 1999, 2000, Scharf & Schlicht 2000). For example, predatory fish often change diet as alternative prey become available (e.g. Moyle & Holzhauser 1978, Shpigel & Fishelson 1989, Silva 1999). However, prey switching extends to species that would not normally be considered to be piscivores. For example, the atherinids *Atherinops affinis* and *Atherinopsis californiensis*, usually thought to be diurnal planktivores, may switch to feed on juvenile engraulids when they are abundant (Coyer & Hall 1993). Prey switching also occurs among the juvenile prey fishes themselves. For instance, juvenile *Sillago maculata* (Sillaginidae) are abundant in shallow waters of northeastern Australian estuaries (Kerby & Brown 1994), where they feed primarily on invertebrate benthos and planktonic crustaceans (McKay 1992, Wilson & Sheaves 2001). Of 264 juvenile (40 to 67 mm) *S. maculata* sampled from shallow waters (<1 m) of 10 estuarine systems on the northeast tropical coast of Australia in July 2000, only 5.3% had consumed fish. However, in 1 individual sample of 10 *S. maculata*, 9 had eaten small (approx. 14 mm) juve-

Table 3. Fishes captured from a tropical estuarine intertidal seagrass bed that had consumed teleost prey (percent occurrence in stomach contents). Modified after Haywood et al. (1998)

Family	Species	Fork length range (mm)	%
Apogonidae	<i>Apogon ruppelli</i>	15–63	1.7
Ariidae	<i>Arius proximus</i>	110–665	24.1
Carangidae	<i>Gnathanodon speciosus</i>	230–360	58.3
	<i>Scomberoides commersonianus</i>	105–880	77.3
Carcharhinidae	<i>Carcharinus cautus</i>	418–1300	77.8
	<i>Rhizoprionodon acutus</i>	418–687	61.3
Chandidae	<i>Ambassis nalua</i>	32–85	20.0
	<i>Ambassis vachelli</i>	17–48	1.4
Engraulidae	<i>Thryssa hamiltoni</i>	85–175	10.7
Gobiidae	<i>Acentrogobius caninus</i>	28–92	10.5
	<i>Butis butis</i>	16–76	4.3
	<i>Drombus palackyi</i>	20–37	5.0
	<i>Favonigobius melanobranchus</i>	17–29	5.3
Leiognathidae	<i>Leiognathus splendens</i>	21–58	1.7
Lethrinidae	<i>Lethrinus lentjan</i>	14–90	10.5
Lutjanidae	<i>Lutjanus russelli</i>	17–140	15.2
Platycephalidae	<i>Cymbacephalus nematophthalmus</i>	69–257	47.8
	<i>Platycephalus indicus</i>	121–410	70.6
Polynemidae	<i>Eleutheronema tetradactylum</i>	290–465	83.3
Serranidae	<i>Centrogenys vaigiensis</i>	14–70	2.2
	<i>Epinephelus suillus</i>	18–270	17.5
Sillaginidae	<i>Sillago lutea</i>	82–210	16.7
Terapontidae	<i>Pelates quadrilineatus</i>	15–180	0.7
	<i>Terapon puta</i>		

nile fishes. Thus because of their abundance in shallow waters and their ability to switch to feeding on fish, juvenile *S. maculata* have the potential to inflict substantial mortality on newly recruited juvenile fishes at times when smaller juveniles are abundant. Clearly, where this occurs extensively, prey switching by the shallow water juvenile fish fauna itself has the potential to greatly extend the impact of predation on small juvenile fishes, particularly during recruitment events.

SAMPLING BIASES

As well as definitional problems, the interpretation of evidence supporting the proposition that there are few piscivorous fishes in shallow estuarine habitats is confounded by a range of potential sampling biases. Rountree & Able (1997) captured substantial numbers of sub-adult and adult piscivorous fishes in the shallow waters of New Jersey estuaries during nighttime sampling. These results contrasted with results of previous studies, suggesting that a lack of nocturnal sampling, together with gear avoidance, may have previously led to underestimates of the abundance of large piscivorous fishes in shallow estuarine habitats (Rountree &

Able 1997). Other studies have reported the potential for biases using gears such as trap, block or weir nets, which are commonly used to sample shallow estuarine habitats. For instance, Robertson & Duke (1990) suggested that large fish may have escaped over their trap nets while the top of the net was submerged, and Cain & Dean (1976) reported escapement from their block net by fish jumping over the net or escaping through holes created by crabs. Additionally, Paterson & Whitfield (2000) suggest that there was some possibility that predatory fish may have escaped from the block net they used in a previous study (Paterson & Whitfield 1996) before or during the deployment of the net. The gill nets often used explicitly to target predators also present problems. They are well known to be very size selective (Henderson & Nepszy 1992), necessitating the use of a range of net sizes for adequate representation (e.g. Blaber et al. 1989). Furthermore, multifilament nets, such as those used by Paterson & Whitfield (2000), are usually much less effective for most species than monofilament nets (Henderson & Nepszy 1992, Matii 1993), providing the potential for poor representation of predator abundance.

Other, perhaps less well-recognised, sampling biases stem from interaction between predator behav-

our and the sampling gear. Predators can be categorised into 2 broad groups: sedentary, ambush predators and active, roving predators (Browman & O'Brien 1992). Each of these modes presents problems for representative sampling. By their very nature sedentary predators are likely to be under-represented in catches using stationary gear such as gill nets, the gear most often used to target larger species in estuaries (e.g. Morton 1990, Robertson & Duke 1990, Rountree & Able 1997, Paterson & Whitfield 2000) (Table 1), because these gears rely on moving fish coming into contact with the net. Thus studies that only employ gill nets are likely to severely underestimate the abundance of such species. The use of apparatus such as seine nets, which sweep an area of bottom, is more likely to produce reliable estimates of the abundance of such species.

Representing the abundances of roving predators is also problematic. Roving predators need only visit an area for a short period of time to inflict considerable mortality on prey fish populations (Hixon & Carr 1997). Thus the average abundance of such species at a site is expected to be very low because they are usually absent. However, it is not the average abundance of predators that is important, rather it is their predatory impact, which might be concentrated in a few minutes once a day or once a week. Consequently, extensive sampling may be necessary to adequately represent the occurrence of such species at a particular site. This problem is exacerbated for schooling species, such as carangids, which are common in sub-tropical (Blaber & Cyrus 1983) and tropical estuaries (Blaber et al. 1989). For schooling, roving piscivores, samples are likely to be characterised by a few large catches and very many zeros. The difficulties in reliably representing the abundance of piscivorous fishes, together with the trophic imperatives that constrain abundance of piscivorous fishes usually to less than the number of fishes at lower trophic levels, mean that much more sampling will usually be needed to adequately represent the abundance of piscivorous species than to represent abundance of their prey. Consequently, although the gill nets used in many studies may be suitable for capturing roving predators, a substantial level of effort may be required to provide adequate representation of their abundance.

DOES 'FEW PISCIVORES' EQUATE TO LOW PREDATION PRESSURE?

I have argued above that limiting the consideration of predation by fishes in shallow waters to large piscivores overlooks the potential for substantial predation by a range of other piscivorous fishes (juveniles of

large piscivorous species, small piscivorous species, and species that can switch to piscivorous feeding when small fish are abundant). However, even when these are included, it may turn out that the abundance of piscivorous fishes in shallow estuarine habitats is indeed low relative to prey species, when compared to other habitats. But does 'few piscivorous fishes' necessarily translate to low predation pressure?

As well as the range of fishes that can contribute to piscivory in shallow estuarine waters, a variety of non-piscine predators have the potential to be important predators on small fishes. Although chaetognaths (Alvarez-Cadena 1993, Baier & Purcell 1997) and copepods (Gao & Li 1992) can feed extensively on larval fish, their predation is largely directed towards small, early-stage larvae. Thus they are unlikely to be major predators for settled juvenile fishes. On the other hand, gelatinous predators, particularly scyphomedusae, can be important predators of late-stage larvae (Cowan & Houde 1991, Breitbart et al. 1994, 1999, Rilling & Houde 1999) and so have the potential to feed on small juvenile fishes. Predation by macrocrustaceans can be substantial. For example, brown shrimp *Crangon crangon* and shore crab *Carcinus maenas* are the main predators of juvenile plaice *Pleuronectes platessa* along the Swedish west coast (Pihl 1990), and blue crabs *Callinectes sapidus* have the potential to cause substantial mortality on mummichogs *Fundulus heteroclitus* in salt marsh pools (Kneib 1982). However, probably the most important non-piscine predators in shallow water habitats are birds (e.g. Mace 1983, Blackwell et al. 1995, Rail & Chapdelaine 1998). For instance, bird predation was responsible for removing ca 30% of sticklebacks in salt marsh pools along the St. Lawrence estuary (Whoriskey & Fitzgerald 1985).

This diversity of potential predators means that the profile of predation (i.e. how total predation is partitioned among different predators) can vary greatly from place to place or time to time. As a result: (1) it is intrinsically difficult to compare predation between places or times simply on the basis of the abundance of 1 or 2 groups of predators; and (2) even at one site the profile of predation may change greatly with depth, without a corresponding change in the overall intensity of predation. For instance, if juvenile fish do use shallow waters as refuges from piscivorous fishes, they may do so at the expense of greatly increased vulnerability to avian predators, such as herons, egrets, gulls and terns (Whitfield & Blaber 1978, Blaber 1987, Raffaelli et al. 1990, Crowder et al. 1997). This complex profile of predation means that it will rarely be possible to imply low predation pressure from observations that there are few piscivorous fishes in an area of shallow water.

CONCLUSIONS

Clearly, the evidence supporting the proposition that there are few piscivorous fishes in shallow estuarine habitats is equivocal. The question is still open and there are substantial difficulties to overcome in answering it. Additionally, asking whether or not large piscivores are common in shallow estuarine waters is not sufficient. Rather it is necessary to consider the whole spectrum of possible predators and how the profile of predation changes in space and time. Moreover, it is necessary to do this in a comparative sense; to compare the relative abundance of predators and prey in shallow estuarine waters to levels in other habitats. Because of the difficulty of sampling all habitats equivalently, and in interpreting information on a range of different predators comparatively, this seems an insurmountable task. Even if these difficulties are overcome, although a comparative approach may provide information about the abundance of predators, it does not really address the important, underlying question: Do small/juvenile fishes using shallow estuarine habitats, gain an advantage because of reduced levels of predator-induced mortality? Clearly this, rather than whether or not predators are abundant in shallow estuarine waters, is the crucial question.

What is required is information on habitat-specific mortality rates. Unfortunately, this information is generally not available (Rountree & Able 1997). Gaining accurate measurements of mortality is very difficult, even at the level of a whole stock (Hilborn & Walters 1992), and trying to obtain individual measures of mortality for different habitats is likely to be much more difficult again. For example, for many prey species it is unlikely that individual fish or groups of fishes occupy only a single area of habitat; rather they are likely to move between habitats (e.g. between high and low tide; Robertson & Duke 1990) and are likely to change their patterns of habitat use over reasonably short periods of time (e.g. over the lunar cycle; Wilson & Sheaves 2001). This makes it difficult to separate changes in numbers due to mortality from changes due to temporal patterns of habitat use. Determining whether predation intensity is really reduced in shallow estuarine areas will require the implementation of carefully designed, imaginative field studies and experiments. For example, using an experimental approach Rooker et al. (1998a) were able to evaluate how habitat complexity influenced the vulnerability of *Sciaenops ocellatus* to predation. Additionally, particularly promising field results were achieved by McIvor & Odum (1988), who used a bioassay approach to compare predation pressure between subtidal habitats with different geomorphologies. In this approach predation pressure was

estimated from the loss of tethered prey fish over time. This approach has been the subject of considerable debate in recent years (Peterson & Black 1994, Aronson & Heck 1995, Pile et al. 1996, Kneib & Scheele 2000, Aronson et al. 2001). However, although further experimental validation is still needed (Kneib & Scheele 2000, Aronson et al. 2001), bioassays have the potential to provide insights that might otherwise be unavailable (Aronson et al. 2001).

CONSEQUENCES AND IMPLICATIONS

The previous discussion aside, a large number of studies have reported low numbers of large piscivorous fishes in shallow estuarine waters (Cain & Dean 1976, Whitfield & Blaber 1978, Shenker & Dean 1979, Blaber & Blaber 1980, Reis & Dean 1981, Rozas & Hackney 1984, Blaber et al. 1985, Morton et al. 1987, McIvor & Odum 1988, Paterson & Whitfield 2000). It certainly makes sense that physical constraints would mean that many large piscivorous fishes would avoid, or be excluded from, very shallow waters (e.g. <0.25 m). If large piscivorous fishes are indeed absent or in low abundances (relative to prey fish densities) in shallow estuarine waters, there are a number of implications. Firstly, there should be an advantage to faster-growing individual prey fish, because they would grow out of the size range vulnerable to small piscivorous fishes (Sogard 1997, Mortensen et al. 2000). Of course attainment of larger size may also mean that depth constraints may force the fish to move to deeper waters, where they are vulnerable to larger predators. Secondly, the absence of large predators may actually be a disadvantage to prey species. For instance, a lack of large predators in shallow waters may permit the maintenance of high abundances of small predators, which would have the potential to inflict a substantial mortality on prey species because of their large numbers and higher requirement for food than their older conspecifics (Yáñez-Arancibia et al. 1994). Thirdly, if there are unusually low numbers of piscivorous fishes in shallow waters, there remains the interesting question of what process would lead to few predators. It is of course possible that it is simply a function of exclusion due to constraints of body size or because of adverse physical conditions (e.g. temperature) in shallow waters, however, there may be other more complex reasons. For instance, just as for prey species, predators face the trade-off between food acquisition and the risk of predation (McPeck 1996, Houston & McNamara 1997). For example, hunting abundant prey in shallow waters may expose the predators to increased risk from terrestrial or avian predators. Whatever the reason, the question goes further than

simple academic interest, because understanding the reason for low abundances of predators in shallow estuarine habitats (when and if this occurs) is pivotal to understanding why, and under what conditions, predation pressure might be reduced. Such understanding is in turn crucial for determining the true nursery ground value of these habitats.

There is also a range of consequences if the use of shallow estuarine habitats does result in reduced levels of predator induced mortality. Firstly, it may be that the advantage of utilising shallow waters is not just an estuarine phenomenon, but common to shallow waters in many marine and aquatic environments. If so, it would be interesting to know if shallow estuarine habitats were more valuable (relative to adjacent deeper water habitats) than, say, shallow areas on coral reefs. Secondly, in a similar vein, do shallow waters with structural complexity (e.g. salt marsh plants, mangroves, macrophytes, seagrass, oyster reefs, snags) perform a similar role/function to shallow, unvegetated habitats (e.g. sand flats, mudflats, saltpans)? Thirdly, is there a difference in the importance of intertidal habitats (which are only available at high tide) and subtidal shallow waters (which may become deep water habitats at high tide) or are the two tightly linked, serving equivalent roles when the other is unavailable? Finally, a greatly reduced predator trophic level suggests that food webs should function differently to those in similar systems with higher predator numbers. For instance, there may be reduced top-down regulation of such food webs (Osenberg & Mittelbach 1996). Many more implications can be envisaged. The variety of these unanswered questions emphasises our poor understanding of many of the biological processes operating in crucial estuarine habitats. Clearly, gaining a detailed picture of the role of predation in shallow estuarine habitats is important in developing a detailed understanding of the functioning of estuaries as nurseries for fishes.

Acknowledgements. I thank Ross Johnston for his insightful comments that added substantially to the quality of this manuscript.

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Editorial responsibility: Otto Kinne (Editor), Oldendorf/Luhe, Germany

*Submitted: April 24, 2001; Accepted: July 26, 2001
Proofs received from author(s): October 18, 2001*