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COMMENT

Predation in littoral habitats is a complex process: Comment on Whitfield (2020)

Ronald Baker[1,2,*], Marcus Sheaves[3]

[1]Department of Marine Sciences, University of South Alabama, Mobile, AL 36688, USA
[2]Dauphin Island Sea Lab, Dauphin Island, AL 36528, USA
[3]Centre for Tropical Water and Aquatic Ecosystem Research, and Marine Data Technologies Hub, College of Science and Engineering, James Cook University, Townsville, QLD, 4811, Australia

ABSTRACT: Shallow littoral waters in estuaries provide important nurseries for a diversity of fish species. The recent review of Whitfield (2020; Mar Ecol Prog Ser 649:219–234) reinforced the long-held paradigm that the value of shallow nurseries is due, in part, to these habitats containing few predators and having low predation pressure. We argue that the provision of refuge does not necessarily mean that a habitat must have few predators and low predation pressure, and present evidence that shallow nurseries contain abundant predator assemblages, may have high predation pressure, and be the habitats where much of the high mortality suffered by juvenile cohorts occurs. Shallow littoral waters are clearly important nurseries, and we highlight the importance of predation in nursery ground functioning.

KEY WORDS: Nursery · Refuge · Piscivore · Estuary

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1. INTRODUCTION

There is overwhelming evidence of the importance of littoral estuarine habitats as nurseries for a diversity of fishes (Beck et al. 2001, Whitfield 2020), and it is essential to protect these habitats (Sheaves et al. 2015, Baker et al. 2020). The recent review by Whitfield (2020) of the nursery function of estuarine littoral habitats builds on a significant and important body of work in this field by Whitfield over many decades. The review reinforces the paradigm that shallow littoral habitats contain few predators and therefore offer the advantage of reduced predation for juvenile fishes. However, our evolving understanding of predation within shallow estuarine habitats suggests that the situation is more complex than fewer predators equaling reduced predation (Sheaves 2001, Baker & Sheaves 2005, 2006, 2007, 2009a,b), and we do not agree with the interpretation of Whitfield (2020) that the presence of small or large piscivorous fishes in shallow habitats compromises their designation as important nurseries. Here, we focus on 2 key issues relating to predation on juvenile fishes in littoral habitats that are central to the conclusions of Whitfield (2020): (1) the identification of relevant predators of juvenile fishes and (2) the interpretation of experimental evidence in support of the littoral refuge paradigm. Rather than few predators and low predation pressure explaining the high densities of juveniles in these habitats, we contend that when considered in the context of population dynamics and lifecycle bottlenecks within interconnected coastal seascapes, shallow water nurseries contain abundant predator assemblages, may be areas of high predation pressure, and are habitats where substantial predation mortality occurs. Shallow littoral habitats may indeed provide refuge that reduces predation mortality on juvenile fishes com-

*Corresponding author: rbaker@disl.org

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pared to mortality rates they would experience if they occupied and were preyed upon in alternate habitats, but it is very challenging to design studies to effectively test this (Baker & Sheaves 2007). Littoral habitats are clearly critical components of estuarine nursery seascapes (Nagelkerken et al. 2015). To understand and maintain the functioning of estuarine nurseries in the face of growing anthropogenic pressures, we feel it is essential to embrace the inherent complexity of these systems and move beyond the overly simplified paradigm that a valuable nursery must have fewer predators and provide measurably lower predation mortality than alternate habitats.

2. WHAT IS AN IMPORTANT PREDATOR?

A key finding of Whitfield's (2020) review is that shallow (<1 m deep) littoral habitats contain few piscivores. However, we contend that this conclusion is based on an incomplete view of what constitutes important predators in these systems (Sheaves 2001, Baker & Sheaves 2005). Whitfield (2020) explicitly restricts consideration to 'taxa whose diet consists mainly of fish' (p. 227) and dismisses the potential importance of the most abundant group of predators in shallow littoral habitats, other juvenile fishes, on the basis that they are small and only occasionally consume fish prey. In contrast, we see substantial evidence that highly abundant small juvenile fishes that occasionally consume other fish probably inflict the bulk of the massive mortality experienced by cohorts of juveniles occupying littoral nursery habitats (Baker & Sheaves 2009b).

Most estuarine-dependent marine species that use littoral habitats as nurseries produce large numbers of offspring that suffer very high rates of mortality during early life, and cohort mortality rates decline through ontogeny (Yáñez-Arancibia et al. 1994, Sogard 1997). Small changes in early mortality rates can have large effects on cohort strength and population sustainability (Levin & Stunz 2005), and heavy predation on newly settled recruits can structure fish communities (Webster 2002, Almany 2004). Recruitment to littoral nursery habitats is pulsed (Robertson & Duke 1990), meaning vulnerable newly settled recruits are only available to predators occasionally. Fish assemblages in littoral nursery habitats around the world are dominated by small juvenile fishes that occasionally consume other fish (e.g. Whitfield & Blaber 1978, Martin & Blaber 1983, Monteleone & Houde 1992, Edgar & Shaw 1995, Garcia et al. 2001, Maes et al. 2003). When we examined the diets of occasional piscivores from shallow littoral habitats in NE Australia, we found that the low average occurrence of fish prey in their diets was a poor reflection of their patterns of consumption of pulsed prey (Baker & Sheaves 2009a). Most of the time these occasional piscivores are supported by alternate prey sources, such as benthic invertebrates (Baker & Sheaves 2005, Whitfield 2020), but occasionally a large proportion of individuals of multiple species will prey heavily on newly recruited fishes (Baker & Sheaves 2009a). These occasional piscivores are so abundant in estuaries that — even if their average diets reflect their impact on fish prey, so that only a small proportion of individuals of these species consumed new recruits — they collectively inflict greater predation mortality on new fish recruits than larger primarily piscivorous fish (Baker & Sheaves 2009b). Many estuarine fish, including predators, will switch their diets in response to food availability (e.g. Whitfield 1984, Elliott et al. 2002). If occasional piscivores do switch to target new recruits during recruitment pulses (Baker & Sheaves 2009a), then their impact on juvenile fishes is orders of magnitude greater than that of larger primary piscivores (Baker & Sheaves 2009b). There is also evidence that the abundance of larger primarily piscivorous fishes has been underestimated in littoral habitats due to gear biases (Rountree & Able 1997, Baker & Sheaves 2006, Whitfield 2020). Rather than being restricted to 'a few selected estuarine systems' (Whitfield 2020, p. 219), small occasional piscivores dominate littoral estuarine habitats around the world (e.g. Whitfield & Blaber 1978, Garcia et al. 2001, Maes et al. 2003). We expect that when similar work to that of Baker & Sheaves (2005, 2009a,b) is done elsewhere, it will confirm that shallow estuarine nursery habitats contain highly abundant and diverse predator assemblages that play important roles in nursery ground functioning (Baker 2006).

3. EXPERIMENTAL EVIDENCE FOR REFUGE

Whitfield (2020) describes experimental evidence to explain the strong associations of small fishes with structured littoral habitats observed in numerous field studies. Laegdsgaard & Johnson (2001) are cited by Whitfield (2020) as providing 'perhaps the most convincing evidence of the refuge function of littoral estuarine macrophyte habitats' (p. 225). This study — like many similar ones — showed that in laboratory mesocosms, small fish retreated into complex habitat when predators were introduced (Laegdsgaard & Johnson 2001). Whitfield (2020) uses these findings to explain that the high densities of small juvenile fishes consistently found within macrophyte-dominated areas of littoral waters is due, at least in part, to the refuge function provided by the complex structure. We agree, however, these experiments also show that in the absence of direct threat of predation, small fish will disperse away from structured habitats (Laegdsgaard & Johnson 2001). Numerous field studies show that small fish show strong affinity for complex structured habitats within shallow littoral waters (e.g. Minello et al. 2008, Smith et al. 2008, Sheaves et al. 2016). This consistent and widespread display of refuge-seeking behavior suggests that there is indeed a substantial risk of predation in shallow littoral waters, otherwise small fish would have no need to seek refuge in complex habitats.

Whitfield (2020) also cites the experiments of Nagelkerken & Faunce (2008) as a demonstration of the refuge value of structured littoral habitats. These experiments showed that juvenile fish assemblages attracted to artificial mangrove units (AMUs) deployed in shallow coastal bays 'collapsed' when the AMUs were removed. The fact that fish which were attracted to a structure subsequently disperse elsewhere when that structure is removed does not prove why they were attracted to it in the first place. The broader point, however, is that although some aspects of littoral habitats, such as complex structures or shallow depths, provide survival advantages to small and juvenile fish by providing refuge from predation, this provision of predation refuge does not mean that valuable nursery habitats must have fewer predators and lower predation pressure than alternate habitats. Rather it indicates that the availability of refuges and predation reduction behavior are important in nurseries (as they are for all life stages) and that there must be predators in the system to drive this response.

4. CONCLUSION

Juvenile fishes have made use of shallow littoral habitats for many millions of years (Gess & Whitfield 2020, Whitfield 2020). Of the large numbers of juveniles that recruit to littoral estuarine nursery habitats, the vast majority do not survive their time in the nursery, because most are eaten. Predators will forage in habitats where food is abundant and available (MacArthur & Pianka 1966), so unless the very high rates of mortality suffered by juvenile life stages are primarily the result of individuals straying from protective littoral habitats, this foraging strategy suggests that predators have evolved for a very long time to consume prey within shallow littoral waters. Littoral nurseries contain abundant and diverse assemblages of piscine predators that will, at times, consume other small juvenile fish occupying the nursery. Therefore, we propose that rather than being habitats with few predators and low predation pressure, littoral nursery habitats are the places where most of the very high predation mortality of juvenile fishes occurs. We can examine patterns of predation pressure under current distribution patterns and behaviors of both predators and prey, but we cannot quantify what the distribution and magnitude of predation pressure would be if juvenile fishes occupied alternate nurseries (Baker & Sheaves 2007). In evolutionary terms, the survival advantage of occupying shallow littoral habitats need only be slight to drive the distribution patterns seen globally, and due to coevolution of predators and prey (Abrams 2000), we should not expect that advantage to necessarily translate into lower predation pressure in the occupied habitats compared to alternate habitats.

Almost 40 years ago, Boesch & Turner (1984) noted that although the roles of food and refuge in shallow estuarine habitats were almost universally accepted, there was little evidence to demonstrate these roles. Today that situation remains, with few demonstrations of enhanced growth or reduced mortality for small fish in littoral habitats (Lefcheck et al. 2019). If we recognize these habitats as parts of dynamic interconnected ecosystems where nursery function is the result of interacting processes at multiple spatial and temporal scales (Sheaves et al. 2015), then it is hardly surprising that we do not have more evidence to support these simple concepts. We recognize the importance of reducing complex natural systems into tractable models that describe general patterns and processes. However, the paradigm of few predators and reduced predation pressure in littoral estuarine habitats is overly simplified and does not capture the extent of predation or its role in nursery ground functioning. Once we understand better how predation regulates populations and structures energy flows and food webs in shallow nurseries and the seascapes in which they are embedded, i.e. the functioning of these critical systems, we will have a greater ability to protect this function into the future (Baker et al. 2020, Gilby et al. 2020, Sheaves et al. 2020).

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