Variability in abundances of fishes associated with seagrass habitats in relation to diets of predatory fishes

Abstract The spatial, diel and tidal variability in the abundance of piscivorous fishes and their teleost prey, and the dietary composition of predatory fishes were investigated in beds of *Heterozostera tasmanica* within Port Phillip Bay, Australia, from September 1997 to February 1998. Predatory and prey fish assemblages were sampled from beds of *H. tasmanica* at three locations during each combination of diel (day and night) and tidal (high and low) cycles. Pelagic and benthic crustaceans represented >60% by abundance of the diets of all predatory fishes. Seven species, 54% of all predatory fishes, were piscivorous. These piscivores consumed individuals from seven families, 36.8% of the fish families being associated with seagrass. Western Australian salmon, *Arriris truttacea* (Arripidae) (*n* = 174) and yank flathead, *Platycephalus speculator* (Platycephalidae) (*n* = 46) were the most abundant piscivores. *A. truttacea* consumed larval/post-larval atherinids, gobiids and sillaginids. *P. speculator* consumed late-juvenile/adult atherinids, clinids and gobiids. While the abundances of piscivores varied between locations (*P* < 0.001) and diel periods (*P* = 0.028), the relative differences in piscivore abundance between sites and diel periods were not consistent between tides. The abundances of *A. truttacea* varied in a complex way amongst sites, diel period and tidal cycle, as shown by a three-way interaction between these factors (*P* = 0.026). During the day, abundance of *A. truttacea* was the abundance of *A. truttacea* significantly higher during high than low times (*P* < 0.001). During the other diel periods at each site, the abundance of *A. truttacea* did not vary. *P. speculator* was significantly more abundant nocturnally (*P* = 0.017). The abundance of small (prey) fishes varied significantly amongst sites (*P* < 0.001). During the day, the abundance of small fishes did not vary between high and low tides (*P* = 0.185), but their nocturnal abundance was greater during low tide (*P* < 0.001). Atherinids (*n* = 1732) and sillaginids (*n* = 1623) were the most abundant families of small fishes. Atherinids were significantly more abundant nocturnally (*P* = 0.005) and during low tides (*P* = 0.029), and varied significantly amongst sites (*P* < 0.001). Sillaginids varied significantly only amongst sites (*P* < 0.001). Seagrass beds provide a foraging habitat for a diverse assemblage of predatory fishes, many of which are piscivorous. Anti-predator behaviour and amongst-location variability in abundances of piscivorous fishes may explain some of the diel and tidal, and broad-scale spatial patterns in small-fish abundances.

Introduction

Exogenous processes, external biological or physical characteristics of the environment, may significantly influence fish populations by increasing mortality (Heath 1992). One of the major causes of natural mortality in fish assemblages is piscivory, predation by other fishes (Hixon 1991). Piscivorous fish may influence the assemblage structure of prey fishes directly by increasing mortality (Wright et al. 1993; Bailey 1994; Fuiman 1994; Juanes and Conover 1995; Connell 1996), or indirectly by modifying fish behaviour and/or other biological interactions such as competition (Sih et al. 1985; Steele 1997). However, the susceptibility of fishes to piscivory depends on prey:predator size ratios (Sogard 1997), diel
activity (Connell 1998), local abundances, and overlap in distributions (Ellertsen et al. 1995; Gotceitas et al. 1996), and physical characteristics of the local environment (Nelson and Bonsdorff 1990; Gotceitas et al. 1997).

To evaluate the importance of piscivorous fishes in structuring prey assemblages, data are needed that describe which species are predators and which are prey (Choat 1982). This is usually accomplished by stomach-contents analysis (Hyslop 1980), but the number of predators needed and the timing of collections to accurately determine the occurrence and representation of common prey in their diets must be considered carefully (Connell and Kingsford 1997).

Once the piscivores are identified, temporal and spatial descriptions of their abundance can provide insight into patterns of impact (Connell and Kingsford 1997). Estimates of the abundances of piscivores amongst locations, and diel or tidal periods within locations, can provide a framework for predicting where and when fish mortality is likely to be heavy (Connell 1996). Amongst locations, the variability in prey-fish assemblage structure may reflect the local abundance of predatory fishes and the direct level of mortality they impose (see review in Hixon 1991). Within locations, variability in the assemblage structure of prey fishes between diel or tidal cycles (Gibson et al. 1998) may reflect anti-predator behaviours (Gibson and Robb 1996) and variability in predation risk (Keats 1990; Sogard and Able 1994; Gibson et al. 1996).

The importance of piscivory in structuring fish assemblages within seagrass beds is largely inferred from studies documenting trophic relationships between predatory fishes and their prey (Robertson 1984; Edgar and Shaw 1995a). Most studies have sampled a single predatory fish or sampled fish at a single time of day and tide or at a single location, despite broad-scale spatial variability in fish assemblage structure (Bell et al. 1988; Jenkins and Wheatley 1998; Jenkins et al. 1998). No studies have assessed the abundance of both predatory fishes and their fish prey over the same spatial, diel and tidal scales, and described the dietary composition of predatory fishes, within seagrass habitats.

Our study investigated the spatial (amongst sites), diel (day vs night) and tidal (high vs low) patterns in predatory and small (prey) fish assemblage structure in seagrass beds in Port Phillip Bay, Australia. Our study also described the diets of predatory fishes, with a view to identifying the importance of seagrass-associated fishes to piscivorous species. These data allowed us to assess the potential for piscivorous fishes to generate spatial, diel and tidal patterns in prey-fish assemblage structure.

**Materials and methods**

**Study sites**

Port Phillip Bay (Fig. 1) is a large (1950 km²), circular, semi-enclosed tidal embayment (Black et al. 1993), joined to the ocean of Bass Strait by a narrow rocky entrance. Except near the entrance, tidal currents within Port Phillip Bay are weak (Black et al. 1993), and there is little thermal or chemical stratification (Longmore et al. 1990). The tides in Port Phillip Bay are semi-diurnal, with a range of <1 m.

Variable-sized beds of the seagrass *Heterozostera tasmanica* (Martens ex Aschers.) den Hartog occur intermittently around the shallow, <5 m deep, margin of Port Phillip Bay. These beds commonly occur as narrow (20 m wide) subtidal bands running parallel to the shore. Beds of *H. tasmanica* are progressively more extensive toward the western side of Port Phillip Bay, which is protected from the prevailing south-westerly weather. *H. tasmanica* beds within Port Phillip Bay are an important nursery habitat for a diverse assemblage of fishes (Jenkins et al. 1997b; Jenkins and Wheatley 1998).

Our study investigated the spatial (amongst sites), diel (day vs night) and tidal (high vs low) patterns in predatory and small (prey) fish assemblage structure in seagrass beds in Port Phillip Bay, Australia. Our study also described the diets of predatory fishes, with a view to identifying the importance of seagrass-associated fishes to piscivorous species. These data allowed us to assess the potential for piscivorous fishes to generate spatial, diel and tidal patterns in prey-fish assemblage structure.

**Field sampling**

Fish assemblages were sampled during each combination of site, diel period (day/night) and tide (high/low) on four separate, haphazardly selected, occasions between September 1997 and February 1998. Sampling was conducted during this period because it coincides with a peak in the abundances of seagrass-associated fishes (Jenkins and Wheatley 1998). Because of the diverse nature of fish...