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Associations between the abundance of piscivorous fishes and their prey on coral reefs: implications for prey-fish mortality

Received: 30 April 2000 / Accepted: 22 September 2000

Abstract Few studies have examined predator-prey relationships in diverse communities such as those found on coral reefs. Here we examined patterns of spatial and temporal association between the local abundance of predator and prey fishes at Lizard Island on the Great Barrier Reef, Australia. We predicted that the nature of this association would have implications for patterns of prey-fish mortality. Strong positive relationships between prey and piscivore abundance were found throughout the study. Greater densities of predators and of prey were found on patch-reef habitats, compared with contiguous reef-slope habitats. Declines in prey-fish abundance on patch reefs were density-dependent and correlated with the densities of predators. The relative roles of recruitment and piscivore movement in determining patterns of predator and prey abundance were assessed from surveys of recruit densities and an intensive programme of tagging two species of rock-cod, Cephalopholis cyanostigma and C. boenak (Serranidae), over 2 years. Patterns of recruitment explained little of the variation in the abundance and distribution of piscivorous fish. If movement explains large-scale patterns of distribution, this was not evident from the tagging study. The two rock-cod species were highly sedentary, with individuals on patch reefs seldom moving among reefs. Individuals on reef slopes were also highly site-attached, although they moved greater distances than those on patch reefs. Although the mechanisms responsible remain to be determined, this study demonstrated strong associations between the abundance of piscivorous fish and their prey on coral reefs. This relationship appeared to be an important factor in producing density-dependent declines in the abundance of prey.

Introduction

One of the central goals in ecology is to determine the causes of temporal and spatial variation in the abundance and distribution of organisms (Menge and Sutherland 1987). Predator-prey interactions can potentially determine the abundance and distribution of predators and prey (Hunter and Price 1992; Menge 1992). It has been argued as a general rule that predator abundance will be limited by prey availability and that prey abundance may be regulated by predators (Hairston et al. 1960; Menge and Sutherland 1976). If predator abundance is limited by prey availability then predator abundance can be predicted to vary in response to fluctuations in prey abundance.

Along with long-term effects on overall population size, prey abundance may have short-term effects on the local abundance (distribution) of predators (Krebs and Davies 1978; Begon et al. 1986). Numerous studies, on a wide range of taxa, have shown that predators tend to concentrate in patches of greatest food or prey availability (the aggregative response) (Krebs and Davies 1978; Werner et al. 1983; Begon et al. 1986; Eklov 1997). Such aggregation of predators in areas of high prey abundance may be maintained by the continual re-location of predators as prey abundance fluctuates in space and time (Hassell and May 1974). The nature of the relationship between predator and prey abundance will depend on the dynamics of the interaction, however (Begon et al. 1986). If there is a short time lag in the interaction, then a positive relationship between predator and prey abundance can be expected, whereas a longer time lag may show the opposite result.
The effects of predators on prey mortality or abundance have also been demonstrated many times (Sih et al. 1985). Aggregation of predators at high-density patches of prey may lead to density-dependent mortality that can in turn regulate prey abundance (Krebs and Davies 1978; Begon et al. 1986). The effects of predators on prey and the reciprocal effects of prey on predators have been recognized most readily in low-diversity communities where food webs are relatively simple (e.g. Menge 1992). Whether or not generalizations can be extended to complex communities composed of diverse assemblages of predator and prey species is unknown.

Patterns in the distribution and abundance of fishes in highly diverse coral-reef habitats have been well documented (Goldman and Talbot 1976; Williams and Hatcher 1983; Williams 1991). Most of the studies investigating the factors causing variation in the abundance of coral-reef fishes have concentrated on small species (Doherty and Williams 1988; Jones 1991). This work has highlighted the importance of a number of interacting processes, including variation in levels of recruitment (Doherty 1981; Victor 1983, 1986; Doherty and Fowler 1994), competition (Jones 1987, 1990, 1991; Robertson 1996), predation (Doherty and Sale 1985; Hixon and Beets 1993; Hixon and Carr 1997), and movement (Robertson 1988; Lewis 1997; Ault and Johnson 1998). Mortality of small fishes is thought to be primarily due to piscivorous fishes which may be a diverse and abundant component of the reef fish fauna (Hixon 1991). Piscivorous species exhibit considerable spatial and temporal variation in their abundance (Williams and Hatcher 1983; Connell and Kingsford 1998; Stewart and Beukers 2000). However, the factors affecting the distribution and abundance of piscivorous fishes are poorly understood. Likewise, few studies have examined the reciprocal effects of predator-prey interactions on predatory fishes and on their prey populations on coral reefs.

There is some evidence that piscivorous reef fish tend to be concentrated in areas of live coral and high relief, such as caves and ledges (Hobson 1965; Huntsman and Waters 1987; Parrish 1987; Connell and Kingsford 1998), as these provide suitable shelter holes. It would also seem likely that attraction of predators to these areas is linked to the high abundance of prey fishes that may be concentrated in similar habitats (Bell and Galzin 1984; Roberts and Ormond 1987; Ault and Johnson 1998). However, the few studies that have examined the relationship between piscivore and prey density in coral reef fish have produced contrasting results. Two studies have found piscivore abundance to be positively related to the abundance of prey (Kock 1982; Beukers and Jones 1997), whereas Hixon and Beets (1989, 1993) found no relationship between predator and prey abundance but a negative correlation between predator abundance and the maximum number of prey on a reef.

The processes establishing these different patterns may relate to the patterns of recruitment and behaviour of different predatory species. Piscivorous fish rarely recruit in high numbers (Shpigel and Fishelson 1991a; Beets and Hixon 1994; Lewis 1997) and it is unknown whether or not they preferentially settle at sites of high prey density. The high mobility of many piscivorous species (e.g. Sweatman 1984; Davies 1995; Samoilys 1997; Zeller 1997a, b, 1998) raises the potential for predators to aggregate at sites of high prey density. Many predators also undergo gradual shifts in their use of habitats as they grow (Eggleston 1995; Light and Jones 1997). On the other hand, competitive interactions among predators may limit their densities at these sites (Begon et al. 1986; Clark et al. 1999). Although there is increasing evidence that patterns of distribution and abundance of reef fishes can be determined by movement, even on isolated reefs (Robertson 1988; Lewis 1997; Ault and Johnson 1998), movement is likely to be more important for larger, predatory species. This needs to be substantiated by intensive tag and release programmes (e.g. Chapman and Kramer 2000).

The relationship between predator and prey abundance may also be influenced by the degree to which piscivores impact the abundance of their prey. Patterns of mortality in coral-reef fish populations have previously been linked with variation in predator abundance (e.g. Caley 1995a; Connell 1996, 1998a). Where predator-induced mortality is density-dependent, predators can regulate prey numbers on coral reefs (Forrester 1995; Caley et al. 1996; Hixon and Carr 1997).

This study examined relationships between the local abundance of piscivorous reef fishes and their prey at Lizard Island on the Great Barrier Reef, Australia. The spatial and temporal association between predators and prey was examined both within and between patch-reef and contiguous reef-slope habitats. We predicted that piscivore and prey abundance would be positively related, owing to the aggregation of predators at high-density patches of prey, and that this in turn would lead to density-dependent mortality of prey fishes. Patterns of recruitment of piscivores and prey, and the movement of two piscivorous species of rock-cod, Cephalopholis cyanostigma and C. boenak (Serranidae), were then examined in detail to investigate their influence on relationships between predator and prey abundance. Rock-cods of the genus Cephalopholis are known to be territorial (Shpigel and Fishelson 1991b; Mackie 1993), but little is known about their long-term movement or how this may be affected by prey density. Lewis (1997), however, suggested that they often moved between isolated patches of reef over periods of months to years. We predicted that the movement of rock-cods within contiguous-reef habitats, and between patch reefs, would correspond to fluctuations in the abundance of prey during the study.

**Materials and methods**

The study was conducted on the western (predominantly sheltered) side of Lizard Island (14°40′S; 145°28′E) on the northern Great Barrier Reef, Australia, between February 1995 and March 1997.