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Effect of simulated macroalgae on the fish assemblage associated with a temperate reef system

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ABSTRACT

Increased habitat complexity is supposed to promote increased diversity, abundance and biomass. This study tested the effect of the macroalgal cover on temperate reef fishes by mimicking macroalgae on artificial reefs in NW Sicily (Mediterranean Sea). Macroalgal cover affected reef fishes in different ways and independently of intrinsic temporal trends. The fish assemblages of manipulated and control artificial reef units differed in the relative abundances of the associated species, but little in species composition. In line with studies in seagrass habitats, fishes were most abundant in reefs covered by artificial macroalgae. Three species (*Boops boops*, *Serranus scriba* and *Symphodus ocellatus*) exhibited consistently greater abundance on vegetated reef units than on control reef units. The total number of species and the abundance of three particular species (*S. scriba*, *S. ocellatus* and *Thalassoma pavo*) displayed temporal trends which were independent on short and large temporal scales. Only fish total biomass and one species (*Spicara flexuosa*) displayed strong effects of interaction among the experimental factors. Mechanisms to explain these findings are discussed from observational evidence on habitat use and interactions among multiple species. This study highlights that manipulative experiments involving repeated sampling of fish in artificial habitats appear to be a valid approach to study fish-habitat relationships in fluctuating environments. It is also concluded that macroalgae mimics may serve as a tool for restoring lost marine vegetated habitats when current human-induced conditions prevent the recovery of pristine macroalgal stands.

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1. Introduction

Increased habitat complexity has long been recognised to exert a positive influence on the diversity and abundance of marine organisms. Habitat complexity promotes resource partitioning by ameliorating competition (Schoener, 1974), and leads to stabilization of predator–prey dynamics (Sih, 1987). Structural complexity (sensu McCoy et al., 1991) is provided by plants in most ecosystems by means of their density and form (Silvertown, 2004). Thick vegetation is still permeable for small or appropriately shaped animals whilst larger or unsuitably shaped species are physically excluded. Hence vegetative cover is frequently used for refuge and foraging under predation risk (Lima and Dill, 1990).

In temperate shallow aquatic environments, vascular macrophytes and macroalgae supply the bulk of the habitat complexity above the bottom (Ebeling and Hixon, 1991). These marine vegetated communities support more diverse and abundant fish assemblages than surrounding unvegetated areas of similar depth, and share many common species irrespective of vegetation type (Jenkins and Wheatley, 1998; Guidetti, 2000). This suggests that many fish species select the structure provided by vegetation rather than specific vegetative species (Heck et al., 2003). Indeed, field experiments indicate that plant volume and cover are among the most important factors driving the structure of temperate fish assemblages (Choat and Ayling, 1987; Carr, 1989), and are particularly important for small-bodied fishes (Shulman, 1985; Carr, 1989; Adams et al., 2004; Crawley et al., 2006).

The effect of plant complexity on fishes may be explained by habitat related resource availability (Jones, 1991). The type of resource also exerts great influence on species-specific and size-specific interactions (Werner et al., 1983b; Persson and Eklöv, 1995). Shelter and food are the most important niche axes in fishes (Wootton, 1998) and many species exploit both resources in vegetated habitats (Lenanton and Caputi, 1989; Crawley et al., 2006). When several resources are present in multiple habitat types, vegetated areas are still preferred by some species, thus it is supposed that their individual fitness is improved there (Werner et al., 1983a; Alofs and Polivka, 2004). More usually, predation refuge and food occur in distinct, alternate habitat types. The role of plant cover as refuge then takes precedence in the presence of predators (Werner et al., 1983b; Shulman, 1985; Gerking, 1994).

How predation success is affected by habitat complexity is strongly species dependent (Diehl, 1988; Eklöv and Diehl, 1994). In general,

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pursuit predators experience reduced foraging efficiency with increases in plant density (Savino and Stein, 1982; Diehl, 1988; Persson and Eklöv, 1995), which can lead to avoidance of complex habitats with low profitability (Werner et al., 1983a; Levi and Francour, 2004). By contrast, ambush predators are largely unaffected by variations in plant density (James and Heck, 1994) up to some critical threshold, after which they too may experience reduced predation success (Savino and Stein, 1989; Persson and Eklöv, 1995).

The behavioural plasticity of fishes (Savino and Stein, 1982; James and Heck, 1994) and the dramatic departures from predicted patterns when numerous species interact (Persson and Eklöv, 1995; Casula et al., 2006) highlight the need for better understanding of the effect of macrophyte complexity on fish assemblages. Such understanding is of theoretical and applied interest in, for example, promotion of diversity through resource partitioning (Wootton, 1998) and enhancement of both fish abundance and biomass (Orth et al., 1984; Heck et al., 2003).

Assessing how fishes respond to vegetative cover has generally followed two paths, observation and manipulation. Observational experiments investigating the effects of vegetal complexity on associated fishes must deal with naturally correlated environmental factors including the spatial configuration of the habitat studied (Jelbart et al., 2006) and the characteristics of adjacent habitats (Dorenbosch et al., 2006). By contrast manipulation of the vegetal cover is constrained by the limits of working underwater and the nature of reef fish systems (Hixon, 1991), and studies are frequently conducted on few species, in more conveniently manipulated habitats. These can be tanks (e.g. James and Heck, 1994), enclosures (e.g. Persson and Eklöv, 1995), estuaries (e.g. Jelbart et al., 2006) and shallow waters (e.g. Hair and Bell, 1992). Unfortunately, the constrained conditions that allow manipulation in the above habitats limit their applicability to open water and deeper reef environments (Choat and Ayling, 1987). Artificial reef habitats allow for the study of these scenarios while controlling most environmental factors, thus providing a way to explore structural effects in otherwise unmanageable environments.

This study explores the response of fish assemblages to structural complexity provided by the macroalgal cover in one of the most common Mediterranean subtidal environments, hard substrate on a sandy matrix. It was predicted that fish assemblages would be altered following manipulation of macroalgal cover and that these changes would persist through time. In particular, it was expected that macroalgae cover would promote a change in species composition, as well as an increase in the total abundance and biomass of the associated reef fish assemblages. This would be due to the advantage gained by small fishes that either feed or shelter inside the canopy, such as some wrasses of the genus *Symphodus*, scorpionfishes, combers, gobies and blennies. In contrast, the model predicted little or no change for fishes that are either large with respect to macroalgae (e.g. pursuit piscivorous like amberjack), planktivorous feeders in the water column (e.g. damselfish), or generalist with respect to food and shelter resources (e.g. seabreams). To test these hypotheses, simulated erect macroalgae were added to scarcely covered artificial reef units, and these manipulated units were compared with control reef units at four time periods within a year across two years, to assess how changes in macroalagal cover alter Mediterranean rocky reef fish assemblages.

2. Materials and methods

2.1. Study area

The experiment was carried out at the Alcamo Marina artificial reef area, in the Gulf of Castellammare, NW Sicily (Fig. 1). The area contains 32 pyramid-shaped units (hereafter called pyramids) made up of concrete blocks (D'Anna et al., 1994). Pyramids were irregularly deployed on an extensive sandy bottom of gentle slope between 1986 and 1995 (Fig. 2). Other artificial reef areas exit in the Gulf of Castellammare, holding benthic communities that differ among areas due to an environmental gradient mainly driven by distinct sedimentation rates (Badalamenti et al., 2002). Such large scale variability in environmental and biotic variables is not detectable within the much smaller spatial scale here studied. The benthic assemblages of the pyramids are characterized by pioneer organisms. These are mainly bryozoans, the endolitic bivalve *Gastrochaena dubia*, the gastropods *Bitium* spp., serpulids and spirorbids. Algae cover is scanty, ranging between 10 and 30% of the pyramid horizontal surfaces, and is dominated by *Halopteris* spp. and *Jania rubens* (Badalamenti et al., 2002 and references therein). The fish assemblages associated to the artificial reefs and surrounding areas have been exploited by artisan fishermen since shortly after reef deployment, speargun fishing and angling are observed during the warm season but trawling is banned within the gulf. As with benthic communities, the fish assemblages differ among different reef areas within the entire gulf (Vega Fernández et al., 2008), but appear homogeneous at the much smaller scale of the present study area. The water column is usually stratified in summer, while in winter storms provoke sediment resuspension and enhanced run-off from land.

Uniformity of fish assemblages was checked prior to the start of the experiment by sampling once at each pyramid in summer 2000 and testing for statistical differences among the future experimental groups.

2.2. Experimental design

The experimental hypotheses were: First, fish assemblages will differ between pyramids with high and low macroalgal cover; second, reefs largely covered by macoalgae will support more algae-dwelling species vulnerable to predation than those with scarce macroalgae coverage; third, the predicted patterns will be consistent through time despite intrinsic fluctuations. A manipulative repeated measures (RM) experiment was designed to test the hypotheses, as the availability of experimental units was limited and the effort needed to manipulate them large. The following factors were considered: treatment (Tr) was a fixed between-subject factor, with three levels: added macroalgae (A), unmanipulated control (C) and control of the manipulation artifacts (R). Pyramid (P) was the subject factor, random and nested within treatment, with 3 levels or experimental units: pyramid 1 (P1), pyramid 2 (P2) and pyramid 3 (P3). Year (Y) was a fixed within-subjects factor, with two levels: first year (Y1) and second year (Y2). Time (Ti) was another within-subject factor, fixed, with four levels separated by periods of about 40 days: early spring (ESP, [a few days of appropriate weather centred around April 13); late spring (LSP, around May 28); early summer (ESU, around July 13) and late summer (LSU, around August 28). It was known from previous work in the study area that three samples per treatment were enough to detect large differences among fish assemblages. To include more replicates would require more time on each sampling occasion, which in turn would mean longer intervals between successive times. The sampling effort was thus allocated so as to yield high temporal resolution when comparing the main structure of the assemblages under different treatments, rather than to gain a detailed depiction of those assemblages on each sampling occasion. One single observation was collected at each pyramid at every sampling time, giving one replicate per cell.

This design implicitly assumes that pyramids were similar. Since there is no formal test for the effect of the subject factor in RM designs, care was taken in selecting a subset of 9 identical pyramids. Criteria for identifying such experimental units were: being at between 14 and 16 m depth and separated by ≥50 m from the closest neighbour, displaying the same physical structure (i.e. without missing, fallen or turned over blocks), as well as orientation and surrounding environment. The appropriate manipulations were then carried out on these pyramids from December 2000 to February 2001.

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