
Potential of Marine Reserves to Cause Community-Wide Changes beyond Their Boundaries

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Abstract: *Fishing and other human activities can alter the abundances, size structure, and behavior of species playing key roles in shaping marine communities (e.g., keystone predators), which may in turn cause ecosystem shifts. Despite extensive evidence that cascading trophic interactions can underlie community-wide recovery inside no-take marine reserves by protecting high-level predators, the spatial extent of these effects into adjacent fished areas is unknown. I examined the potential for community-wide changes (i.e., the transition from overgrazed coralline barrens to macroalgal beds) in temperate rocky reefs within and around a no-take marine reserve. For this purpose I assessed distribution patterns of predatory fishes, sea urchins, and barrens across the reserve boundaries. Predatory fishes were significantly more abundant within the reserve than in adjacent locations, with moderate spillover across the reserve edges. In contrast, community-wide changes of benthic assemblages were apparent well beyond the reserve boundaries, which is consistent with temporary movements of predatory fishes (e.g., foraging migration) from the reserve to surrounding areas. My results suggest that no-take marine reserves can promote community-wide changes beyond their boundaries.*

Keywords: alternative community states, community-wide changes, marine reserves, overfishing, temperate rocky reefs, trophic cascades

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Resumen: *La pesca y otras actividades humanas pueden alterar la abundancia, tamaño, estructura y comportamiento de las especies que juegan papeles clave en el modelado de las comunidades marinas (e.g., depredadores clave), que a su vez pueden causar cambios en los ecosistemas. No obstante la evidencia extensiva de que las interacciones tróficas en cascada pueden subyacer en la recuperación de la comunidad dentro de reservas marinas que no permiten la pesca mediante la protección de depredadores de nivel alto, se desconoce la extensión espacial de estos efectos en áreas adyacentes. Examiné el potencial de los cambios a nivel comunidad (i.e., la transición de áreas coralinas sobre pastoreadas a lechos de microalgas) en arrecifes rocosos templados dentro y alrededor de una reserva marina sin pesca. Para este propósito, evalué los patrones de distribución de peces depredadores, erizos de mar y áreas sobre pastoreadas en los límites de la reserva. Los peces depredadores fueron significativamente más abundantes dentro de la reserva que en localidades adyacentes, con un excedente moderado en los bordes de la reserva. En contraste, los cambios a nivel de comunidad en los ensambles bénticos fueron aparentes más allá de los límites de la reserva, lo que es consistente con los movimientos temporales de los peces depredadores (e.g., migración de forrajeo) desde la reserva hacia las áreas circundantes. Mis resultados sugieren que las reservas que no permiten la pesca pueden promover cambios a nivel comunidad más allá de sus límites.*

Palabras Clave: arrecifes rocosos templados, cambios a nivel comunitario, cascadas tróficas, estados comunitarios alternativos, exceso de pesca, reservas marinas

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Introduction

Increasing concern over the consequences of human exploitation of natural resources at sea has led, in recent decades, to the proposal of ecosystem-based management tools (Pikitch et al. 2004). In coastal areas worldwide, fishing is one of the most significant human impacts on populations, habitats, and whole communities (e.g., Tegner & Dayton 2000; Jackson et al. 2001; Myers & Worm 2003). No-take marine reserves (i.e., areas of the ocean protected from extractive uses) have become important tools for management and conservation of marine communities (Tegner & Dayton 2000). Results of empirical studies show increased density and/or size of target species within reserves compared with fished areas (Halpern & Warner 2002; Halpern 2003), spillover of fish across reserve boundaries (Roberts et al. 2001; Abesamis & Russ 2005), and community-wide changes following fishing bans (Castilla & Durán 1985; Sala et al. 1998; Shears & Babcock 2003; Micheli et al. 2004). Such effects are mostly attributable to protection from fishing, which directly affects high-level predators and indirectly affects entire communities (Pinnegar et al. 2000; Jackson et al. 2001).

In many temperate reefs worldwide, removal of sea urchin predators has been demonstrated to release sea urchins from predator control (Breen & Mann 1976; Estes & Duggins 1995; Sala et al. 1998; Pinnegar et al. 2000; Witman & Dayton 2001). The related increase in density of sea urchins (the most important grazers in temperate regions) can potentially cause the transition of an area from macroalgal stands and forests to coralline barrens and loss of ecosystem functions (Tegner & Dayton 2000; Shears & Babcock 2002). Recovery of predators within reserves may reverse this community shift (Shears & Babcock 2003).

In Mediterranean subtidal rocky reefs, adult sea urchins (*Paracentrotus lividus* and *Arbacia lixula*) are effectively preyed on by only a few fish species, especially the sea breams *Diplodus sargus* and *D. vulgaris* (Sala et al. 1998; Hereu et al. 2005; Guidetti 2006), which are strongly targeted by fishers (Harmelin et al. 1995; Coll et al. 2004). The relationship between such fish predators and sea urchins can be affected by a variety of factors, such as the predator size relative to prey size (Guidetti 2006), availability of shelter (Sala et al. 1998; Hereu et al. 2005), wave action (Micheli et al. 2005), and the substrate type (Guidetti et al. 2005a). Sea urchins released from predatory control due to overfishing of predators can achieve high densities and cause the transition of the community from macroalgal beds to barrens (Sala et al. 1998; Guidetti 2006). Recovery of fish predators and reestablishment of lost trophic interactions within marine reserves may reverse this community shift (Guidetti 2006). It is important to determine whether these effects are localized (i.e., occur only within the protected areas)

or whether the potential movements of predatory fishes beyond the reserve boundaries may cause community-wide changes in adjacent areas. I sought to provide evidence for possible community-wide changes in sublittoral rocky reefs by examining distribution patterns of predatory fishes and sea urchins, and the extent of barrens across the boundaries of a Mediterranean marine reserve.

Methods

Torre Guaceto Marine Reserve (TGMR) is located in southeastern Italy (southern Adriatic Sea; Fig. 1). The study area is generally characterized by a rocky plateau with a gentle-to-medium slope, declining from the water surface to about 10 m over coarse sand. The TGMR covers about 2220 ha (entirely a no-take area at the time the study was done) and was formally established in 1992, although enforcement started being successful some years later when effective control by local authorities and reserve personnel began (Guidetti 2006). Professional and recreational fishers fish outside the reserve, including areas close to reserve boundaries (Guidetti et al. 2005b). Although there has been no quantitative assessment of the local fishing impact, fewer than 10 small professional fishing boats are active in the areas outside and surrounding the reserve, where trammels, gillnets, traps, and lines with hooks are used. The impact of spearfishing and recreational fishing from boats is moderate. No diving is done in or surrounding the reserve. A recent study provided an indirect assessment of the fishing impact. The comparison of fishing yield inside and outside the TGMR showed that quantities of commercial fishes extracted from the protected area with trammels were roughly fourfold greater than those obtained outside the reserve (Vierucci et al. 2006).

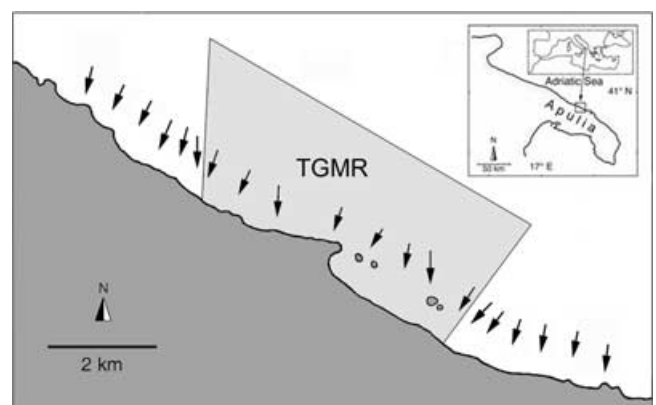


Figure 1. Study location and sampling sites (arrows) inside and outside the Torre Guaceto Marine Reserve (TGMR).

In the past before the reserve was established and actually protected, there were large sea urchin barrens in the area presently included in the reserve and where rocky reefs are now largely dominated by macroalgae (Guidetti 2006). This community shift, mediated by the reestablishment of fish predator pressure on sea urchins within the reserve (Guidetti 2006), suggests that any difference detected between the reserve and fished areas at Torre Guaceto (e.g., fishery yield, fish predator density) is mostly attributable to effective protection and not to the fact that the specific areas included in the reserve were already originally different or special.

In May–July 2004 I used scuba to assess the density of sea breams and sea urchins and the extent of barrens in rocky reefs 4–7 m deep. Ungrazed benthic communities in the area are largely dominated by macroalgae (mainly turf or erected algae; Guidetti 2006), so cover of barrens is the variable that may best represent the overgrazed alternate condition. Fish density was evaluated by means of visual census (along strip transects of 25×5 m; Harmelin-Vivien et al. 1985), whereas sea urchin density and barren extent were assessed within quadrats (1×1 m). Each fish census and sea urchin and barren quadrat survey was replicated 160 times. Sea urchin and barren quadrats were surveyed for densities of sea urchins and the extent of barrens (percentage), respectively, at 20 sites: 8 within the TGMR (extending from the center to the northern and southern boundaries) and 12 in adjacent fished areas (6 beyond the northern reserve boundary and 6 beyond the southern boundary up to a distance of approx. 2 km from the edges of the reserve; Fig. 1).

I examined correlation between pairs of variables at each site sampled with Pearson correlation and then used logistic function (see Kaunda-Arara & Rose 2004 for details) to describe how fish and sea urchin density and barren extent changed from the center of the TGMR with distance across the northern and southern boundaries. The regression model was tested with the log-transformed data. Slopes (mean change in the variables per unit change in distance from the reserve center) and inflexion points (distance from reserve boundaries at which maximum values are halved) of the logistic curves were used to investigate gradients of density or cover across the reserve boundaries.

Results

Sea bream and sea urchin densities were negatively correlated across different sites ($R = 0.53$; $p < 0.05$; $n = 20$). The correlation between sea urchin density and barren extent was highly positive ($R = 0.92$; $p < 0.001$; $n = 20$).

The density of predatory fishes declined across the northern and southern reserve boundaries (northern

boundary: slope = -0.003 , inflexion point = -459.7 , $F = 32.0$, $p = 0.0005$; southern boundary: slope = -0.001 , inflexion point = -755.8 , $F = 25.3$, $p = 0.001$). Negative values of the inflexion point reveal that maximum *Diplodus* density at the center of the TGMR halved inside the reserve at approximately 450–750 m from the boundaries (Fig. 2a). In contrast, gradients of sea urchin density increased from the reserve center to the fished areas outside the TGMR (north: slope = 0.003 , inflexion point = 309.6 , $F = 12.6$, $p = 0.007$; south: slope = 0.005 , inflexion point = 305.0 , $F = 10.66$, $p = 0.011$). The positive values of the inflexion point show that maximum sea urchin density observed in fished areas declined by 50% at approximately 300 m outside the boundaries of the TGMR (Fig. 2b). Spatial gradients of barrens were similar to those of sea urchins (north: slope = 0.002 , inflexion point = 235.7 , $F = 9.44$, $p = 0.015$; south: slope = 0.006 , inflexion point = 209.9 , $F = 10.52$, $p = 0.012$). The maximum values measured in fished areas were half that at approximately 200–250 m outside the boundaries of the TGMR (Fig. 2c).

Discussion

The density of *Diplodus* fish was far higher inside the TGMR than outside. The difference was dramatic and is likely to be due to protection from fishing (i.e., the so-called reserve effect; Halpern 2003). *Diplodus sargus* and *D. vulgaris* are targeted by many kinds of fishery (commercial and recreational: lines with hooks, spearfishing), and the reserve effect is particularly significant for target species in the Mediterranean Sea (e.g., Guidetti 2006; Guidetti & Sala 2007) and elsewhere (e.g., Micheli et al. 2004). From this perspective, enforcement at TGMR is effective (see Methods), and the reserve has been protected long enough to encompass the life span of *Diplodus* fish, which can live up to 10 years (Froese & Pauly 2004). Protection within the TGMR is thus likely to have allowed *Diplodus* populations to recover in terms of both density and size at levels high enough to effectively control sea urchin populations and indirectly trigger the transition from coralline barrens back to macroalgal beds within the reserve (Guidetti 2006).

Field experiments documented far higher fish predation rates on sea urchins inside the TGMR than outside (Guidetti 2006). The above issues suggest there may be changes at population and community levels within marine reserves following a fishing ban. The community-wide recovery after reestablishment of predatory trophic interactions within reserves could involve predatory fishes moving from the reserve and feeding on sea urchins outside the reserve at a rate high enough to significantly reduce grazing and allow macroalgal

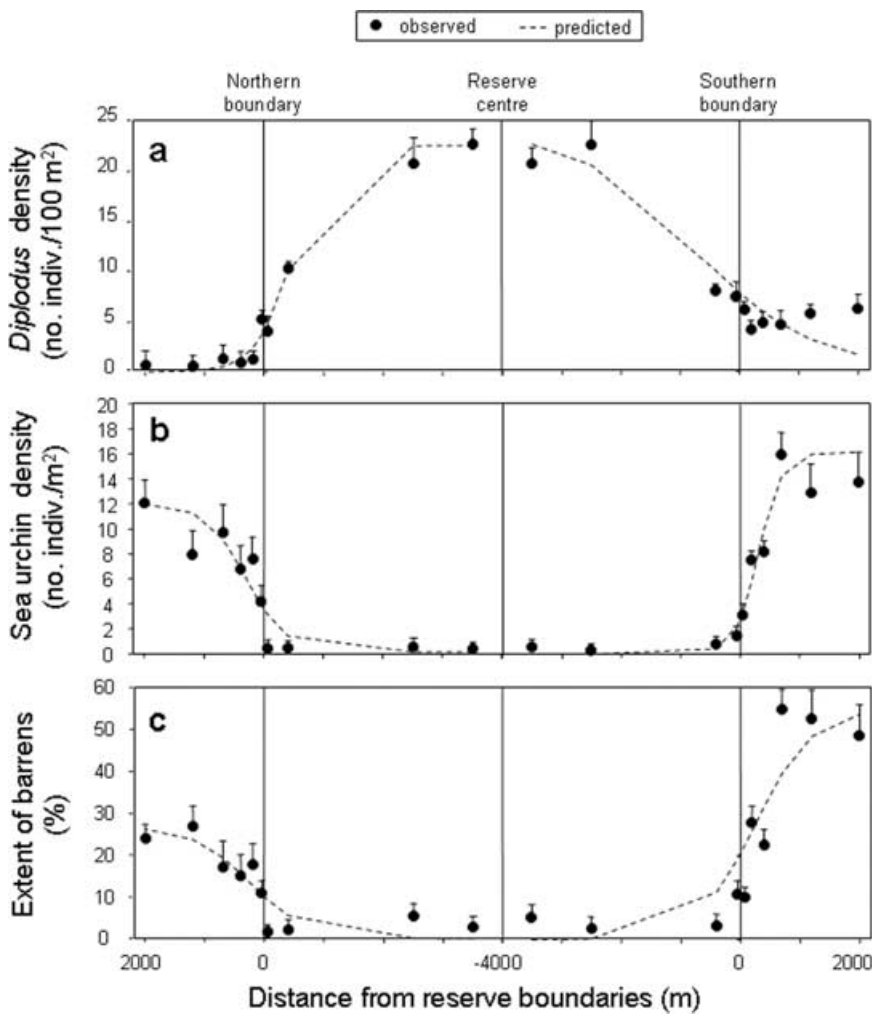


Figure 2. (a) Density of *Diploodus* (a fish predator of sea urchins), (b) density of sea urchins, and (c) extent of barrens across the boundaries of the Torre Guaceto Marine Reserve (mean \pm SE).

recolonization. Daylight distribution patterns of predatory fishes I observed, nevertheless, suggest a moderate spillover (in terms of passive density-dependent diffusion) from the TGMR and a substantial concentration of *Diploodus* within the reserve. Maximum densities of *Diploodus* observed at the center of the TGMR were half that amount well inside the reserve boundaries and decreased abruptly within a few hundreds of meters outside the reserve. Similar declines of fish density around the reserve edges seem to be common to many reserves worldwide (Kaunda-Arara & Rose 2004), although differences among species may occur depending on the catchability, mobility, and other traits of species (Rakitin & Kramer 1996; Ashworth & Ormond 2005).

Distribution patterns of target fishes across reserve boundaries, however, should be interpreted with caution. At several marine reserves worldwide, fishing activities concentrate outside the reserve and close to the boundaries in order to benefit from the spillover of fish (Abesamis & Russ 2005). This implies that patterns of fish density around the reserve boundaries are the result of the superimposing effects of biomass exportation and

exploitation (Halpern et al. 2004). This is not likely to be the case, however, at the TGMR, where a relatively small number of professional and recreational fishers operate outside the reserve, close to the boundaries. As suggested by Halpern et al. (2004), the export of increased production from within the reserve tends to offset the effects of displaced fishing effort in conditions of low fishing pressure at the reserve edges. Additionally, visual censuses of fishes are usually made in daylight (Harmelin-Vivien et al. 1985), and patterns of *Diploodus* density observed at the TGMR showed that fishes tend to concentrate inside the reserve. Ecological effects of fish predators (i.e., sea urchin population control and consequent abundance of macroalgal beds), however, appeared to extend well beyond the reserve boundaries (up to 500–1000 m from the edges). Therefore, movements of fishes caused by processes other than density-dependent spillover, such as foraging migration of fishes from the reserve toward and beyond its edges at times when visual censuses are not done (at dawn, night, or sunset), could explain the patterns I observed. This hypothesis is supported by data of fish catches around the TGMR (P.G., unpublished data).

that show that *Diplodus sargus* and *D. vulgaris* actively move from sunset to dawn when they forage, as reported by other authors (Lloret & Planes 2003).

Finally, the patterns I observed were evidently asymmetric between the northern and southern boundaries. Although habitat types (e.g., rocky substrates, sands, and sea grasses) are approximately the same at the two reserve boundaries, I could not exclude a priori that differences in the relative cover or patchiness of different habitats may affect, to some extent, movement patterns of fishes, distribution of urchins and algae, and consequently their interactions. Ecological interactions within marine reserves and the "halo" effect of marine reserves on community structure in areas adjacent to a reserve are complex but central issues that are receiving increasing attention from conservation ecologists (Langlois et al. 2006).

My results, therefore, highlight the importance of combining static evaluations of effects of marine reserves (e.g., based on comparisons of patterns between reserves and fished areas; e.g., Shears & Babcock 2003; Guidetti 2006) with experimental and mechanistic studies of the dispersal and behavior of key species (e.g., density-dependent migration and habitat use of predators) and provides the first evidence that marine reserves may have the potential to cause ecosystem-wide changes beyond their boundaries.

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