Fish diversity components and community-wide changes: an experimental case study in the Mediterranean rocky sublittoral

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In the last decades there has been an increased concern about species loss (or functional loss of species) and introduction of new species into ecosystems. Attention was mostly devoted to changes in ecosystem properties due to changes in diversity of primary producers (or other low-level species in food webs) both in terrestrial and aquatic systems.
In general (with a few exceptions), diversity was found to enhance productivity and stability.

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The number of papers published about the marine fish diversity loss has also dramatically increased in the last years...

... with special emphasis on the impacts of human disturbances, particularly **fishing** that chiefly affects high level predatory fishes.
Fish diversity loss and ecosystem functions and stability ... not only large predators are important

Loss of herbivore fishes may have dramatic effects in coral reef ecosystems

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Fish assemblages from Bahamian coral reefs (159 species): limited redundancy and potential for widespread fishing impacts

1) 1/3 of functional groups include 1-2 species
2) Fished species in all but two functional groups
3) All species are fished in 1/2 of functional groups

(F. Micheli, unpublished data)
Many fishes targeted by fishing are, however, high level predators. Predator species loss may disrupt food webs due to usually low redundancy and typical life traits, and affect ecosystem functioning more than plant diversity loss.
Evolutionary implications

Fishing selection has been proposed to oppose natural selection for size, behavior, morphology, maturity status, with potential consequences on demography, stock biomass, economic revenues, competitive and predator-prey interactions.

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Community-wide effects

Besides direct effects on target species, fishing may affect entire communities (and ecosystem functioning) through changes in trophic interactions, e.g. the so-called trophic cascades (top-down control).
Not only species loss …

In many regions of the world, fish communities are changing due to climate changes (e.g. water warming) and, sometime, ‘new’ species appear … increasing the species richness and potentially influencing both native species and assemblages through interactions.
Mediterranean Sea and water warming

The basin in the last decades underwent tropicalisation (new tropical-atlantic and indopacific species appeared) and meridionalisation (southern species expanding northwards)

- Thalassoma pavo
- Sargocentron rubrum
- Fistularia commersoni
- Sphoeroides marmoratus
- Siganus luridus
- Sparisoma cretense
The Mediterranean rocky sublittoral

There is increasing evidence that fishing (also interacting with other processes e.g. sedimentation and water warming) may have community-wide effects similar to those occurring in kelp forests.
The protagonists

Sea urchins, through unselective grazing, may form and maintain *barrens*, especially at high density

Sea breams may eat small and relatively large sea urchins

Labrids may eat small urchins (<1 cm test size)

Professional and recreational-sportive fishing impact sea urchin fish predators
Marine reserves may help ecosystem recovery

Predation levels estimated by tethering experiments

MarINE RESERVES REESTABLISH LOST PREDATORY INTERACTIONS AND CAUSE COMMUNITY CHANGES IN ROCKY REEFS

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Abstract. In the last decades, marine reserves have dramatically increased in number worldwide. Here I examined the potential of no-take marine reserves to reestablish lost predatory interactions and, in turn, cause community-wide changes in Mediterranean rocky reefs. Protected locations supported higher density and size of the most effective fish prey.
Predator size matters!

Small predators eat only small prey, large predators may exploit a wide range of prey sizes.
Predator density and size thus rule predator-prey interactions and community structure in the Mediterranean rocky sublittoral ... but what about predator diversity?

In terrestrial systems, multiple predators may have linear or non-linear ecosystem-wide effects.

Such experimental studies, however, are not that common in marine systems.
Assemblages of fish predators change in space, e.g. along latitudinal gradients.

Correlative observations suggest the higher predator diversity the higher grazer density and barren extent … but here possible ‘diversity effects’ are *confounded* with climatic conditions changing with latitude.
Diversity components and experiments

1) Number of species present (species richness)

2) Relative abundances (impacts more often affect evenness than presence/absence)

3) Species identity: particular species can have strong–idiosyncratic effects on community and/or processes

How to cope with all this?

Increasing accuracy of causal inference in experimental analyses of biodiversity

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Summary

1. Manipulative experiments are often used to identify causal linkages between biodiversity and productivity in terrestrial and aquatic habitats.
2. Most studies have identified an effect of biodiversity, but their interpretation has stimulated considerable debate. The main difficulties lie in separating the effect of species richness from those due to changes in identity and relative density of species.

Fig. 2. Illustration of a possible alternative to the null hypothesis of no effect of SR in the presence of negative density-dependent effects. The effect of adding one unit of B to one unit of A differs in magnitude and direction from the effect of adding one unit of A. This would be detected by a significant interaction between SR and density.
Manipulative experiment using caging

1) What can we predict in the case of species loss or addition?
2) Do the four predator species interact?
3) Does capacity of controlling sea urchin density change relative to predator diversity and/or density (additive vs interactive effects)?

- Juvenile sea urchins (40x40 cm)
- Adult urchins (1x2 m)
- Coris adults
- Thalassoma adults
- Diplodus vulgaris
- Diplodus sargus

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Rationale

Caging experiments were repeated in two bays (spatial replication)

In each bay, EUs 5x5 m were prepared according to 6 treatments: (1) no predators (control), (2) *C. julis*, (3) *T. pavo*, (4) *D. vulgaris*, (5) *D. sargus*, and (6) the complete assemblage of the four predators

Experiment 1: additive design, with density of each predator species equivalent to the values measured in the field (INTRA-specific interactions constant)

Experiment 2: substitutive design, with overall predator density kept constant

N=3 replicates for each treatment in each bay for both design type

Response variable: PREDATION RATE ON SEA URCHINS

Data treated with ANOVA: 1) ‘treatment’, fixed; 2) ‘bay’, random orthogonal
Emerging impacts of multiple predators

To solve the additive problem in summing the relative impacts of multiple predators on prey, I used the *multiplicative risk model* (Sih et al. 1998).

Additive or emergent effects of multiple predator guilds (i.e. wrasses and sea breams) on sea urchins were tested by comparing the observed predation risk to the predicted values generated by a null model, i.e. the *MRM*, using a two-way ANOVA: “treatment” (three levels: wrasses, sea breams, wrasses + sea breams) and the categories “observed vs expected” (two levels) were treated as fixed and orthogonal factors.
Patterns were coherent between the two bays

**Experiment 1 (ADDITIVE)**

<table>
<thead>
<tr>
<th>Treatment</th>
<th>No predators</th>
<th>Coris julis</th>
<th>Thalassoma pavo</th>
<th>Diplodus vulgaris</th>
<th>Diplodus sargus</th>
<th>All predatory species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Proportion of prey eaten</td>
<td>(A) Juvenile sea urchins ( (F_{(5,5)} = 87.5, P &lt; 0.001) )</td>
<td>c</td>
<td>c</td>
<td>b</td>
<td>b</td>
<td>a</td>
</tr>
<tr>
<td></td>
<td>(B) Adult sea urchins ( (F_{(5,5)} = 42.6, P &lt; 0.001) )</td>
<td>b</td>
<td>b</td>
<td>b</td>
<td>a</td>
<td>a</td>
</tr>
</tbody>
</table>

In treatments with ‘all predators’ there is the max species richness, but also max density

**Experiment 2 (SUBSTITUTIVE)**

<table>
<thead>
<tr>
<th>Treatment</th>
<th>No predators</th>
<th>Coris julis</th>
<th>Thalassoma pavo</th>
<th>Diplodus vulgaris</th>
<th>Diplodus sargus</th>
<th>All predatory species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Proportion of prey eaten</td>
<td>(A) Juvenile sea urchins ( (F_{(5,5)} = 136.5, P &lt; 0.001) )</td>
<td>c</td>
<td>c</td>
<td>c</td>
<td>a</td>
<td>a</td>
</tr>
<tr>
<td></td>
<td>(B) Adult sea urchins ( (F_{(5,5)} = 43.7, P &lt; 0.001) )</td>
<td>b</td>
<td>b</td>
<td>b</td>
<td>a</td>
<td>b</td>
</tr>
</tbody>
</table>

Total density constant, but predator assemblage composition changes

The two labrid fishes, and the two sparids have the same effects … they can be treated as two guilds

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An emerging impact (negative) of multiple predators has been observed only for adult sea urchins

- Non-additivity intraguild (density-dependence) and non-additivity interguild are similar
  - 1 or 2 guilds have the same effects on predation rates
- Non-additivity intraguild and non-additivity interguild are NOT similar
  - 2 guilds cause a decrease in predation rates
Final remarks

Cascading effects of fish predator removal on entire communities (observed worldwide) suggest that decreasing predator density may disrupt natural communities.

There is increasing evidence, however, that there is no linear relationship between functioning and species richness, but that different species may have idiosyncratic effects.

This study experimentally stressed:

1) the major contribution from sea breams to predation upon sea urchins in rocky reefs compared to that from wrasses (species identity vs species richness);
2) the foraging efficiency of sea breams decreases in the presence of wrasses (interference competition)

Null, positive or negative effects of multi-predator assemblages on prey and communities depend on the relationships among predators (interference, intra-guild predation, facilitation)

From this perspective, the finding that increasing wrasse density may decrease the capacity of the fish predator assemblage to control sea urchin populations and, consequently, formation of barrens is of some concern

*T. pavo* is increasing in the Med. Water warming could thus affect species interactions and enhance desertification of rocky reefs in the Mediterranean Sea

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**Abundance and size structure of Thalassoma pavo (Pisces: Labridae) in the western Mediterranean Sea: variability at different spatial scales**

Paolo Guidetti*, Carlo Nike Bianchi¹, Gabriele La Mesa¹, Milena Modena¹, Carla Morri¹, Giampietro Sara¹ and Marino Vacchi²

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Manipulative experiments can help provide guidelines to interpret effects of biodiversity loss or elucidate species roles and the effects of diversity components on processes, but they are possible only in limited cases and for limited temporal scales.

Although with weaker inference, historical ecology is a valid tool to understand the effects of diversity loss in multispecies systems where predictive approaches are not unanimously accepted.
Whatever the focus of any study (e.g. fishing management, conservation), understanding the effects of changes or losses in marine biodiversity and the related causal processes (e.g. fishing or climate changes) represents the most exciting challenge for any marine ecologist in these days.

Thank you for your attention.