Long-term change in a meso-predator community in response to prolonged and heterogeneous human impact

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Sharks and rays’ abundance can decline considerably with fishing. Community changes, however, are more complex because of species interactions, and variable vulnerability and exposure to fishing. We evaluated long-term changes in the elasmobranch community of the Adriatic Sea, a heavily exploited Mediterranean basin where top-predators have been strongly depleted historically, and fishing developed unevenly between the western and eastern side. Combining and standardizing catch data from five trawl surveys from 1948–2005, we estimated abundance trends and explained community changes using life histories, fish-market and effort data, and historical information. We identified a highly depleted elasmobranch community. Since 1948, catch rates have declined by 94% and 11 species ceased to be detected. The exploitation history and spatial gradients in fishing pressure explained most patterns in abundance and diversity, including the absence of strong compensatory increases. Ecological corridors and large-scale protected areas emerged as potential management options for elasmobranch conservation.

Analyses of exploited fish communities in coastal, demersal and pelagic ecosystems have shown that elasmobranch (sharks and rays) diversity and abundance can decline considerably after only short periods of fishing1–3. For example, in the Northwest Atlantic, catch rates of 18 large pelagic and coastal shark declined by 49–89% in less than 15 years2. In South Africa, large coastal sharks were reduced by 27% - >99% after 20 years of shark netting programs3, and in Southeast Australia, 20 years of trawling reduced demersal elasmobranch catch rates by >80%3. Industrial bottom trawl fisheries in particular can have strong effects on demersal communities by unselectively catching a wide range of species while destroying complex seafloor habitats4,5.

Aside from declines in population abundance, shifts in community composition can occur because fishes have different intrinsic vulnerabilities to exploitation, are unequally exposed to fishing, and respond to changes in predators and competitors. Any species is characterized by an intrinsic rebound potential ($r$), a population parameter that combines a set of biological traits (maturity, fecundity, and growth) determining the species productivity and capacity to sustain exploitation6. As a group, elasmobranchs generally have very low $r$ values due to their late sexual maturity, low fecundity and slow growth rate, hence they are unable to sustain even moderate levels of exploitation7,8. Yet even among elasmobranchs, $r$ is variable enough9,7 to sometimes explain observed differences in the species’ response to fishing10,11. In other cases, variable exposure to fishing12,13,3 and changes in the abundance of predators and competitors12,14–17 have been more important predictors of community change.

Predation is an important factor explaining meso-predator population dynamics and community changes in terrestrial18 and aquatic ecosystems19. Among elasmobranchs, large sharks are the main predators of smaller sharks and rays20. While many large sharks have declined over the last decades, meso-predatory elasmobranchs have increased in exploited communities of the Atlantic21,17,15,12, Pacific22,3 and Indian Ocean23,24. However, the magnitude and trajectory of population increases are not always predictable because prey benefit from both reduced natural mortality and a reduced risk of predation25,26. The latter is a more pervasive but not easily quantifiable behaviorally-mediated effect that influences prey distribution, habitat and food choices, and overall fitness3. Moreover, while sharing common predators, sympatric species compete for limiting resources, which influence their abundance. When fishing or other human impacts selectively deplete or removes species26, releases from competition are often predicted and were suggested to explain unexpected increases in elasmobranchs in
several areas, of the world\textsuperscript{21,16,17,27}. Yet in some of these cases, alternative explanations, such as shifts in spatial distribution, also played a role\textsuperscript{28}.

Explaining community changes in large marine ecosystems by identifying the occurrence and relative contribution of direct and indirect effects of fishing, or other human impacts, is challenging because it requires performing controlled experiments impractical at large scales. In these cases, adopting an observational approach across gradients of natural or human-induced perturbations is an efficient alternative\textsuperscript{19}. We used such an approach to study the long-term changes in the elasmobranch community of the Adriatic Sea, whose long history of human-induced changes, as well as the spatial and temporal contrasts of perturbations, offered an ideal case study. The Adriatic Sea is a semi-enclosed Mediterranean basin that has been exploited for thousands of years, and where large marine predators (sharks, pinnipeds, and cetaceans) have declined dramatically over the past two centuries\textsuperscript{29}. The Adriatic’s broad continental shelf and accessible fishing grounds allowed the development of large fisheries for shellfish and groundfish\textsuperscript{30}. Yet fisheries developed unevenly between the western and eastern sides of the basin. While Italian waters were exposed to extremely high exploitation pressure from high-capacity fishing fleets, former Yugoslavian sectors sustained a much lighter fishing exploitation until recently (see Supplementary Methods for a brief fishing and ecosystem depletion history).

To examine spatial and temporal changes in the elasmobranch community, we used data from five different scientific trawl surveys carried out in the Adriatic since 1948 (Fig. 1, Table 1). First, we extracted species-specific trends of catch rates to estimate short-term community changes within surveys. Then we estimated long-term community changes comparing catches across surveys. Finally, we used life-history characteristics, environmental factors (e.g. sediment composition, temperature), fishing effort data, and historical fishing information to explain the observed trajectories of population and community changes. It was our aim to identify the main drivers of change, whether the decline of large predatory sharks triggered meso-predator releases, and if there was a change of the elasmobranch community composition suggesting competitive interactions.

### Results

In total, 2575 tows carried out over six decades across the Adriatic Sea detected 33 small, demersal, meso-predatory elasmobranch species (average trophic level: 3.9, SD: 0.12\textsuperscript{31}), including 12 sharks, 20 rays and one chimaera (included for their evolutionary and ecological similarity, Table 2). Of these, 11 species ceased to be detected during the period of observation (no more occurrences after the year 2000, Table 2), while 6, mostly deep-water species and small skates, were only recently detected by the MEDITS surveys which expanded to greater sampling depths (Table 2).

![Figure 1](https://www.nature.com/scientificreports/)

**Figure 1 | Positions of tows performed during the surveys analyzed in the Adriatic Sea.** Survey details are in Table 1 and Supplementary Table S1.
Across all five surveys, species-specific frequency distributions were very skewed (Fig. 2), with few dominant species and many occurring only sporadically. The Hvar survey detected the highest diversity (23 species, Shannon Index [SI]: 3.39, Fig. 2a), dominated by small-spotted cat sharks and thornback skates with unstandardized densities of 426.8 and 76.8 individuals/km², respectively, and frequencies of occurrence (FO) of 0.76 and 0.71. The other 21 species were caught in < 21% of the tows with densities below 11 ind./km². Over time, moving to the most recent survey, richness and abundance decreased toward more flattened and truncated distributions. In MEDITS (SI: 1.96), the small-spotted catshark was still the most abundant species, but with a density of 62.1 ind./km² and FO of 0.021 and densities < 4 ind./km². The high elasmobranch abundance and diversity characterizing the central Adriatic during the Hvar survey in 1948–49 disappeared (Fig. 3a and b). Yet, species richness and abundance were higher in the eastern coastal areas than elsewhere (Fig. 3a and b). Elasmobranch abundance in Croatia was almost one order of magnitude higher than in Italy (Supplementary Fig. S1), where sharks and rays were largely absent except for a relatively high-density zone in the upper Adriatic (above the 50 m isobath, Fig. 3a). MEDITS mainly composed of spurdogs (Supplementary Fig. S2), smooth-hounds, and eagle rays.

Standardized catches generally confirmed the above patterns. Although the fitted models had considerable selection uncertainty - in each survey, more than half of the species had a selected best model with <10% chance (Akaike weight <0.1) of being the most

### Table 1: Trawl surveys

| Survey      | Time range | Sampling design | Depth range | Tows | Stations | Species | Index of abundance |
|-------------|------------|-----------------|-------------|------|----------|---------|--------------------|
| Hvar        | 1948–1949  | ASBS            | 20–433.5    | 278  | 167      | 23      | n/tow              |
| Zupanovic   | 1957–1958  | RA              | 29.5–104    | 126  | 10       | 17      | n/tow              |
| Jukic       | 1963–1971  | Hvar stations   | 38–262      | 197  | 24       | 15      | n/tow              |
| GRUND       | 1994–1995  | Transect SRS    | 13–421      | 307  | 75       | 13      | n/hour             |
| MEDITS      | 1994–2005  | SRS             | 9.5–840     | 1667 | 144      | 27      | n/tow              |

Summary of trawl surveys used for analyses listing the survey's time range, sampling design (ASBS: Adapted to Seabed Suitability; RA: random allocation within the survey domain; SRS: Stratified Random Sampling), depth range (m), number of tows and stations, number of elasmobranch species detected, and the available index of abundance. For GRUND, until May 1995, a SRS scheme was adopted, then the survey switched to a transect design. For data sources see Supplementary Methods.

### Table 2: Species caught in the trawl surveys

| Species                                | Tows | Individuals | First | Last | Drange | Length |
|----------------------------------------|------|-------------|-------|------|--------|--------|
| 1 Heptanchias perlo (sharpnose sevengill shark) | 2    | 2           | 1948  | 1948 | 27–1000| 138    |
| 2 Leucoraja circularis (sandy skate)    | 2    | 2           | 1948  | 1948 | 70–900 | 120    |
| 3 Pteromyxus baurus (bullray)           | 1    | 44          | 1948  | 1948 | 10–150 | 250    |
| 4 Galeorhinus galeus (tope shark)       | 15   | 18          | 1948  | 1957 | 2–450  | 186    |
| 5 Squatina squatinia (angel shark)      | 11   | 16          | 1948  | 1958 | 0–150  | 180    |
| 6 Dipturus batas (common skate)         | 14   | 17          | 1948  | 1968 | 100–1000| 242    |
| 7 Raja radula (rough skate)             | 8    | 8           | 1968  | 1994 | 40–450 | 70     |
| 8 Rhinoptera marginata (ludsonian cownose) | 2    | 2           | 1994  | 1994 | 30–100 | 200*   |
| 9 Dasyatis centroura (rougtail stingray)| 4    | 4           | 1957  | 1996 | 3–270  | 247    |
| 10 Dalatias litchi (kitefin shark)      | 3    | 7           | 1995  | 1997 | 40–1800| 181    |
| 11 Raja polyactis (speckled skate)       | 2    | 2           | 1999  | 2000 | 100–400| 60     |
| 12 Dipturus oxyrinchus (longnose skate)  | 30   | 60          | 1948  | 2001 | 0–900  | 150    |
| 13 Torpedo nobiliana (back torpedo)     | 1    | 1           | 2001  | 2001 | 2–800  | 150    |
| 14 Chlamydoscentra (angular roughshark)  | 1    | 48          | 1948  | 2003 | 60–660 | 150    |
| 15 Torpedo torpedo (common torpedo)      | 2    | 2           | 1996  | 2003 | 0–150  | 50     |
| 16 Chimaera monstrosa (rabbit fish)     | 11   | 71          | 1994  | 2004 | 200–1000| 87     |
| 17 Etmopterus spinax (velvet belly)      | 11   | 57          | 1994  | 2004 | 70–2000| 53     |
| 18 Rostroaja alba (white skate)          | 16   | 18          | 1948  | 2004 | 40–500 | 200    |
| 19 Squalus blainville (longnose spurdog)| 79   | 348         | 1948  | 2004 | 14–1100| 110    |
| 20 Dasyatis pastinaca (common stingray)  | 45   | 94          | 1948  | 2005 | 60–200 | 150    |
| 21 Galeus melastomus (blackmouth shark) | 41   | 1147        | 1948  | 2005 | 50–1000| 68     |
| 22 Leucoraja melitensis (maltese skate)  | 1    | 1           | 2005  | 2005 | 60–800 | 50     |
| 23 Mustelus asterias (starry smooth-hound) | 63  | 94          | 1948  | 2005 | 0–100  | 140    |
| 24 Mustelus mustelus (smooth-hound)      | 186  | 1302        | 1948  | 2005 | 0–350  | 162    |
| 25 Myliobatis aquila (common eagle ray)  | 133  | 539         | 1948  | 2005 | 0–200  | 150    |
| 26 Raja asterias (starry skate)          | 55   | 129         | 1948  | 2005 | 10–300 | 72     |
| 27 Raja clavata (thornback skate)        | 536  | 3612        | 1948  | 2005 | 0–700  | 107    |
| 28 Raja miraletus (brown skate)          | 327  | 1780        | 1948  | 2005 | 50–150 | 66     |
| 29 Raja montagui (spotted skate)         | 9    | 9           | 1948  | 2005 | 0–550  | 77     |
| 30 Scyllorhinus canicula (small-spotted catshark) | 812 | 24401      | 1948  | 2005 | 0–400  | 76     |
| 31 Scyllorhinus stellaris (nursehound)   | 139  | 396         | 1948  | 2005 | 0–100  | 150    |
| 32 Squalus acanthias (spurdog)           | 425  | 3632        | 1948  | 2005 | 10–200 | 125    |
| 33 Torpedo marmorata (marbled torpedo)   | 68   | 92          | 1948  | 2005 | 20–350 | 82     |

Species detected in the Adriatic trawl surveys (1948–2005). Tows are the number of trawl tows that caught the species. Individuals refer to the cumulative number of specimens detected in all tows. First and Last are the years of the first and last catch, respectively. Drange [m] and Length [cm] are the depth distribution range and maximum length of the species reported in the literature (* is disc width).
plausible among a 95% confidence set of models (see methods, Supplementary Tables S2–S6) – spatial covariates (depth, latitude and longitude) resulted as the best predictors of species abundance (Tables 3 and S2–S6). In the largest surveys available (Hvar and MEDITS), these predictors pointed to an increase in catch rates from the Italian to the Croatian coasts, and for most species from deep to shallow waters (i.e. from offshore to inshore, Supplementary Fig. S3).

Temporal covariates (year, time of the year) were less important than spatial variables, but many species had significant short-term temporal trends within surveys (Fig. 4).

Analyses of catches in the Jukic survey (1963–1971), located in the central eastern Adriatic, identified nine species with reliable short-term trends in abundance, and all except the thornback skate showed an increase in catch rates from the Italian to the Croatian coasts, and from deep to shallow waters (i.e. from offshore to inshore, Supplementary Fig. S3). Temporal covariates (year, time of the year) were less important than spatial variables, but many species had significant short-term temporal trends within surveys (Fig. 4).

In the coastal area off the eastern Adriatic (Zupanovic area, Fig. 1), between 1957 and 2005 elasmobranchs increased significantly by 2.12 times (CI: 1.59, 2.83). Rays increased faster than sharks (3.79 vs. 1.88 times) with brown skate and common eagle rays recording fold increases of 17.7 (CI: 9.9, 31.7) and 19.73 (CI: 7.08, 55.03) respectively. As for sharks, the patterns were largely driven by the almost 2-fold increase of small-spotted catsharks (1.92, CI: 1.1, 3.4).

In the Jukic area, comparing catch rates in the period 1948–1971 (Hvar-Jukic comparison), elasmobranchs declined by 61% in 23 years. These were mainly sharks (−95.6% vs. −87.7%) with small-spotted catsharks (−96.2%, CI: −97.8%, −93.5%) driving most of the patterns. Rays shifted in species composition. In particular, the thornback skate, the most abundant ray in the 1940s, recorded the steepest decline (−97.2%, CI: −98.4%, −95%), whereas brown skates increased by 2.36 times (CI: 1.05, 5.3) becoming the most abundant skates (Fig. 2e). Significant long-term increases were also detected for eagle rays (111 times, CI: 17.05, 735), marbled torpedoes (75.9 times, CI: 5.07, 1135.64) and spurdogs (3.1 times, CI: 1.05, 9.27) (Fig. 5a and b).

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The smooth-hound recorded the largest increase (21.13, CI: 8.23, 54.25), and the thornback skate was the only elasmobranch showing a significant decline (−39.8%, CI: −63.14%, −1.77%) (Fig. 5c).
Figure 3 | Spatial comparisons of catches between Hvar and MEDITS surveys. (a) unstandardized CPUEs, and (b) species richness. For MEDITS we selected only the last two years of the series (2004–05) for a balanced temporal comparison. Crosses are tows with no elasmobranchs.

Table 3 | Importance of covariates

| Covariate                    | Hvar (647) | Zupanovic (215) | Jukic (430) | GRUND (215) | MEDITS (1294) |
|-----------------------------|------------|-----------------|-------------|-------------|---------------|
| Longitude east (E)          | 2.62       | 2.53            | 1.87        | 2.55        | 2.89          |
| Latitude north (N)          | 3.56       | 1.41            | 3.33        | 1.91        | 3.32          |
| Depth (D)                   | 3.19       | 2.71            | 3.33        | 3.36        | 2.58          |
| Sediment composition $R_m$  | 4.29       | 4.29            | 4.55        | 5.58        |
| Longitude east (E)$^2$      | 5.56       | 6.12            | 3.93        | 4.64        | 6.37          |
| Temperature (T)             | 5.38       |                 |             |             |               |
| Year (Y)                    | 5.60       |                 |             |             | 5.26          |
| Sediment granulometry $R_1$ | 5.69       | 6.71            | 6.20        | 5.27        | 6.16          |
| Depth (D)$^2$               | 6.94       | 4.94            | 6.67        | 5.82        | 6.95          |
| Time of the year $S_1$      | 5.75       | 6.65            | 5.80        | 6.91        | 8.26          |
| Country (C)                 | 7.40       |                 |             |             | 6.79          |
| Time of the year $S_2$      | 8.25       | 6.59            | 6.47        | 6.55        | 6.89          |
| Bottom category $B$         |            |                 |             |             | 7.40          |
| Temperature (T)$^2$         | 8.56       |                 |             |             | 9.26          |
| Year (Y)$^2$                |            |                 |             |             |               |

Mean rank of covariates selected from the 95% CS of models for the different surveys (sorted in descending order of average importance across surveys). The number of model combinations fitted to the data is in parentheses (models with quadratic terms without their main effects were not evaluated). The set of variables composing the starting models are identified by the rows having non-empty values under each survey heading. Coordinates are in decimal degrees, depth in meters (mean point of each trawl path), and temperature in °C. Bottom sediment composition was categorical in Jukic (B), while it was continuous and expressed as log ratio of percent of mud over sand in Zupanovic, GRUND and MEDITS ($R_m = \log(\frac{m}{s})$), and as log ratio of percent of granulometry categories in Hvar ($R_1 = \log(\frac{c_1}{c_4})$), details in Supplementary Methods. Country (categorical) was included in the models for MEDITS to test the differences between samples carried out by Slovenian, Croatian and Italian research institutes.
skates suggested some increase, and the common eagle ray increased by 128 times (CI: 46, 358). The spurdog was the only shark increasing significantly (4.43-fold, CI: 1.43–13.72), while 4 of the other 5 species we could model recorded declines between ~63% (small spotted cat-shark, CI: ~83.6%, ~16.6%) and ~96.8% (the smooth-hound, CI: ~98.7%, ~92%). In contrast, in the period 1963–2005 (Jukic-MEDITS comparison), sharks and rays as a group declined comparably and significantly by more than 90%. Spurdogs reversed their earlier increase with a decline of ~87.6% (CI: ~95.2%, ~68%) and the increase of common eagle rays became non significant. This time, smooth-hounds recorded the only significant increase (356 times, CI: 6.8, 18534; Fig. 5e).

All these results were robust to mis-specification and uncertainty of trawl performance (in terms of swept area), to sampling and estimation error of sediment composition, and to the surveys’ sample sizes (see Supplementary Methods).

Our projected distribution of current fishing intensity (Fig. 2f) reflected the patterns in abundance and distribution detected in MEDITS (except for the upper Adriatic Sea, Fig. 3), and was consistent with the spatial parameter estimates of the standardized catches (Supplementary Fig. S3). The eastern Adriatic (mainly fished by Italy) has a much lower level of fishing pressure than the western side (exploited by Italy). Italy records about twice the amount of otter trawlers longer than 18 meters is a good index of offshore fishing intensity (between 3 and 40 nautical miles), fishing exploitation is an order of magnitude higher in Italian than Croatian waters (0.005 vs. 0.0003 boats per square kilometer, Supplementary Fig. S4). If the number of otter trawlers longer than 18 meters is a good index of offshore fishing intensity (between 3 and 40 nautical miles), fishing exploitation is an order of magnitude higher in Italian than Croatian waters (0.005 vs. 0.0003 boats per square kilometer, Supplementary Fig. S4).

The intrinsic vulnerability of species did not explain the variability of the observed rates of change. We found no significant relationships between r and $\beta_i$s estimated from MEDITS (slope 0.996, p-value: 0.504, R²: 0.035), Jukic (slope = 3.499, p-value 0.152, R²: 0.27), historical comparisons in the Hvar area (slope = 14.020, p-value: 0.51, R²: 0.039), Jukic area between Hvar and Jukic (slope = 5.91, p-value: 0.75, R²: 0.013), Jukic area between Jukic and MEDITS (slope = 14.53, p-value = 0.45, R²: 0.072) and in the Zupanovic area (slope = 23.61, p-value: 0.18, R²: 0.21).

Discussion

Understanding long-term changes in exploited fish communities requires the consideration of several factors, including the intrinsic vulnerability of various species to exploitation, changes in biological interactions (e.g. predation and competition), different exposure to fishing (e.g. catchability, availability, and commercial value) and susceptibility to other stressors such as habitat degradation and pollution. All of these factors can alter the species-specific response to exploitation, generating complex community changes over time and space. Here, we attempted to understand long-term changes in the allocation of fishing boats per port was proportional to the port population density (Supplementary Materials). Dividing the number of boats fishing in these different Croatian sectors by the sectors’ trawleable surface (i.e. excluding 3 nautical miles from the shores) showed that most of the Croatian channel region would be free from trawling, which instead would take place mostly in the coastal areas (between 3 and 6 nautical miles) of Istria and the outer channel areas (Supplementary Fig. S4). If the number of otter trawlers longer than 18 meters is a good index of offshore fishing intensity (between 3 and 40 nautical miles), fishing exploitation is an order of magnitude higher in Italian than Croatian waters (0.005 vs. 0.0003 boats per square kilometer, Supplementary Fig. S4).

Figure 4 | Short-term trends. Raindrop plot of $\beta_i$s’ profile likelihoods for elasmobranchs detected during the Jukic (1963–1972, a), and MEDITS surveys (1994–2005, b). Drop widths indicate the 95% CI of $\beta_i$. Drop thickness at a particular $\beta_i$ value indicates the relative plausibility of that value. Green raindrops indicate sharks. Orange indicates rays. The rabbit fish is in grey.
Figure 5 | Long-term changes. (a) Long-term changes of standardized CPUEs of elasmobranch species and aggregated groups detected in the Hvar spatial domain (Figure 1) by Hvar and MEDITS surveys. Grey bars (with upper 95% confidence intervals) are standardized CPUEs recorded in the Hvar survey, and red bars are those recorded in MEDITS. The expected CPUEs are calculated for a location correspondent to the average depth of all tows occurring in the comparison area, in mid July. The inset is a magnification of the bars inside the red polygon. (b–e) Centipede plots of catch rate changes (in % relative to initial level or factor of increase) for species (circles) and aggregated groups (triangles) estimated in the long-term comparisons of trawl surveys. The species considered in each panel occurred for three or more years in their respective long-term comparison. Green indicates sharks, orange rays, and grey specifies all elasmobranchs aggregated.
elasmobranch community in the Adriatic Sea and the underlying drivers.

By analyzing trawl surveys carried out in the area over the last six decades, we detected a structurally depleted elasmobranch community. A total of 2575 tows were not sufficient to detect at least 25 elasmobranch species that were recorded in the area before 1948 (Supplementary Table S7). These included 13 great sharks (>2 m in length), which may not have been caught due to their lower trawl catchability compared to demersal species, but also 8 bottom-associated large meso-predatory elasmobranchs (e.g. angelsharks, guitarfishes, large rays, bramble and gulper sharks, Supplementary Table S7), some of which were the target of dedicated fisheries52–54. Most of the 33 species detected by the trawl surveys strongly declined over time, and 11 disappeared, updating the list of possible extinctions in the Adriatic Sea55–57 to 22 species. Overall, sharks declined stronger than rays (−95.6% vs. −87.7%), and more shark than ray species recorded significant declines (4 vs. 2 species respectively, Hvar-MEDITS comparison Fig. 3b). Similar strong depletions of elasmobranch abundance and diversity were recorded in exploited fishing grounds of the North Sea58, southeastern Australia59, the Mediterranean (Fig. 5b). In general, competition and predation releases are more evident when not confounded by high levels of fishing mortality60. Thus, when we compared historical and more recent surveys off central Croatia (Jukic area, Fig. 5d and c), an area where offshore fishing pressure has only recently increased61,62, earlier population increases were later reversed or buffered such as for spurdogs and common eagle rays. Similarly, long-term patterns of change detected over the Hvar area, were different in the less exploited Croatian channels during a comparable time span. There, only thornback skate recorded a significant albeit moderate decline (−39.3% over 48 years, CI: −63.1%, −1.8%) while most of the other species increased (Zupanovic area, Fig. 5 b and c). Thus, compensatory changes might persist in relatively unexploited areas while in other parts were eventually overruled by the effects of exploitation.

Stronger predator or competitor releases might have occurred historically in the 19th and early 20th century, when large predatory sharks (e.g. hammerhead, mako, porbeagle and white sharks) were in decline57–59, but fishing had not yet expanded to industrial levels (Supplementary Methods). At that time, angel sharks, spurdogs, smooth-hounds, and skates were so abundant to sustain targeted fisheries44–46, and the main Adriatic fish markets recorded increases in elasmobranch landings67–69. Such increases were particularly evident after periods of reduced fishing operations (e.g. during the two World Wars) and characterized by exceptional but not biologically plausible catches. For example, in the years immediately following the wars, D’Ancona (1949) described foot-seine hauls of 70–160 smooth-hounds averaging 10 kg a piece in Chioggia, despite the fact that it takes about 16 years for that species to reach such a size (Supplementary Methods). This may suggest compensatory population increases of residential sharks, but also possible immigration of individuals from neighbouring, less-exploited areas. Similar patterns were observed in the North Sea70, and on Georges Bank (NW Atlantic) where the rapid increase of winter skate, previously attributed to competition releases, were related to environmentally driven immigration of individuals from the northern Scotian Shelf71. Differences in species mobility, and thus exposure to exploitation are congruent with the observed patterns of resilience and depletion in the Adriatic. The high densities of bentho-pelagic elasmobranchs (spurdogs, smooth-hounds, and eagle rays) in the heavily exploited upper Adriatic might partly highlight the simplistic nature of our fishing-effort model, but also a possible spillover of mobile species from the underexploited Istria to the heavily fished but extremely productive northern Italian sectors. Specific oceanographic conditions, the influence of the Po River, and strong seasonal fluctuations of oceanographic regimes72 make the upper Adriatic an extremely productive area characterized by a great abundance of benthic (molluscs and crustaceans) and pelagic primary consumers (sardine and anchovies)70, which attract elasmobranchs. Devoid of pelagic larval stages, elasmobranchs disperse relying on intrinsic mobility and available ecological corridors73. The species that were dominant in the upper Adriatic can undertake transoceanic and long seasonal migrations74–76, and have home ranges much larger than the northern Adriatic. Hence they may be little affected by localized stressors because they are able to replenish from areas even outside the Adriatic, possibly using relatively sheltered gateways in Croatian coastal waters. Conversely, elasmobranchs with limited mobility such as catsharks and other skates (home ranges <50 km77,78) persisted in the less-exploited eastern Adriatic and almost completely disappeared from the heavily exploited Italian waters. In summary, the long history of human impacts severely depleted the Adriatic predator and meso-predator community, leaving the ecosystem in a structurally altered state. The elasmobranch
community went through a sequence of population depletions (from great sharks in the 19th and 20th centuries, to large meso-predatory elasmobranchs in the early 20th century to smaller more productive species in the later 20th) and shifts in species composition. More recently, this culminated in the near disappearance of elasmobranchs in the most exploited areas of the Adriatic Sea. Cases of ecological compensation due to release from predation or predation competition were not as evident as in other marine regions and may have pre-dated our observation window. Yet the strong gradient of fishing intensity from the Italian to the Croatian side allowed the persistence of a more abundant and diverse elasmobranch community in the eastern Adriatic, which may fuel a spillover of mobile species toward more exploited western areas. Similar contrasts of decline and resilience of exploited fish populations were observed in large systems of marine protected areas established on Georges Bank and the Great Barrier Reef.

In January 2008, Croatia established a 23,870 km² Ecological and Fisheries Protection Zone (EFPZ) in its national and international waters. However, after 3 months, the EFPZ was dismissed because of harsh opposition of bordering countries. Our results suggest that planned and managed internationally, and concerned with a reduction of fishing pressure in western areas and control of developing fisheries in the east, a similar initiative could protect abundance and diversity of Croatian resources from further depletion. Furthermore, it could promote elasmobranch recovery in the overall Adriatic by profiting from the remaining strongholds of elasmobranch abundance and diversity in the east, otherwise scarcely protected by current marine protected areas.

**Methods**

**Survey data and analytical outline.** Our dataset comprised 2575 trawl tows, from three surveys identified as Hvar, GRUND, and MEDITS, covering large portions of the basin; and two surveys, we called Jukic and Zupanovic, more locally confined to Croatian waters (Fig. 1, Table 1, Supplementary Methods and Table S1).

We initially analyzed each survey individually to avoid dealing with differences in sampling framework and gears, potentially influencing the estimated indices of abundance. We identified the available environmental and methodological covariates explaining most of the catch variability, and used these variables to standardize the catches. We estimated short-term trends in catch rates from surveys having more than three years of observations, and estimated long-term changes by combining historical and recent surveys in overlapping spatial domains. Finally, we attempted to explain the observed spatial and temporal patterns of the catches with data on fishing effort and species life-histories.

**Catch standardization.** Standardization is paramount when combining independent experimental observations (such as this set of surveys) differing in sampling framework, gear specification and survey’s spatial domain (area and depth range). This process avoids inferring false population trends from observed catch trajectories. Also taking into account the inherent density, detection probability, and spatial distribution of a species is necessary to prevent estimating biased indices of abundance. The low population densities of elasmobranchs and their patchy distribution generate catch distributions highly skewed, successfully described with a negative binomial distribution.

GLMs flexibly accommodate unbalanced sampling schemes and non-normal data. Hence using this framework, we assumed that the chance of obtaining a variable with different numerical scales, continuous variables were standardized by using unit normal scaling, \( z = \frac{x - \mu}{\sigma} \), where \( x \) is the mean of variable \( x \) and \( z \) is its standard deviation. To avoid collinearity, correlated variables were discarded or combined into predictors expressing unrelated information.

We needed to identify important predictors, answer ecological questions, and also avoid the identification of spurious relationships resulting from over-fitting a full-saturated model (having 2 parameters, for \( n \) variables, including all interactions of main effects) to small datasets. Therefore we included only main effects and quadratic forms of some continuous variables (Table 3). Quadratic functions of depth, temperature, latitude and longitude were included to capture the tendency of animals to aggregate around optimal values of environmental variables. A quadratic function of year in MEDITS, the survey with the longest time span, was also included to model possible compensatory responses of species to changing exploitation regimes, competition or predation. Higher order temporal polynomials were not attempted, having limited temporal observation windows on animals characterized by slow population dynamics. To capture the habit of many elasmobranchs to undertake in seasonal migrations or shift in distribution, we included a periodic function of survey date, \( S = S_1 + S_2 = \cos \left( \frac{2 \pi t}{365.25} \right) + \sin \left( \frac{2 \pi t}{365.25} \right) \), where \( t \) is the ordinal day for tow \( t \) (referred to the earliest date of all the surveys), which eventually allowed us to compare different surveys for tows performed at different times of the year. Substrate composition was included to account for the strong resilience of demersal species on seabed features.

**Model selection.** From the initial model, for each species, we selected a reasonable preliminary model structure by backward elimination of covariates in SAS 9.1 (Supplementary Methods). This preliminary model was used to estimate the negative binomial dispersion parameters \( k \) to use in a second model selection stage (performed in R 2.15.0), when most variable combinations of the initial model (number is given in Table 3) were refitted by providing the estimated \( k \) as initial values. For each model \( m \), (variable combination) we calculated the Akaike Information Criterion (AIC), AIC differences \( \Delta \) (\( \Delta = AIC_m - AIC_{AICm} \)). Weights \( w_m = \frac{\exp(-1/2 \Delta_i)}{\sum \exp(-1/2 \Delta_i)} \) where \( R \) is the number of models fitted; and evidence ratios \( (w_m/\max w_m) \). We then selected the best model corresponding to the minimum AIC value, and the set of models with AIC differences < 2 to identify a 95% confidence set (CS) of other plausible models. We used this CS to calculate the most important variables to explain the variability of the set, and the overall importance of these variables in explaining the catches of most species. To calculate the importance \( \omega_i \) of a variable \( x_i \), we summed the Akaike weights of all the models containing the variable among the CS, \( \sum w_i \omega_i(l_i) \), where \( l_i \) is 1 if variable \( x_i \) is in model \( m \), 0 otherwise; \( k \) is the number of models in the CS. To evaluate the overall importance of the variables across species, we first ranked the variable importance \( f_k \) for species from 1 (the most important, highest \( w_i \)) to \( n \) (the maximum number of covariates used in a given survey). Then we averaged the ranks across all species.

**Short-term trends.** In Jukic and MEDITS, we estimated a species-specific instantaneous rate of change over time \( \beta \), including year among the set of standardizing covariates regardless of whether it was included in the best model. We profiled the best-model likelihood functions for a range of fixed \( \beta, s (\text{e.g.} -0.9, 0.9, \text{le from 0.99 declines to about 20,000 fold increases}) and selected the value corresponding to the maximum likelihood. Obtaining within-survey trends was important to test the species’ response to current exploitation levels and uncover possible compensatory community changes due to competition.

**Long-term changes.** We combined spatially overlapping surveys to estimate long-term changes in CPUEs for all elasmobranchs combined as well as for all sharks (including rabbit fishes), rays, and individual species. We compared the tows performed to overlapping surveys (including rabbit fishes), rays, and individual species. We compared the tows performed to overlapping surveys (including rabbit fishes), rays, and individual species. We compared the tows performed to overlapping surveys.
projected over the Adriatic. By using data on number, horse power (HP), and gross tonnage (GT) of boats fishing along the Adriatic coasts, we assumed that the intensity of fishing per unit of sea bed surface (at any point in the Adriatic Sea) was proportional to the cumulative effort exerted by all Adriatic fishing fleets, whose individual contribution depended on the distance between any point and the fleet harboring port, fleet size, and point bathymetry. Using empirical data of effort distribution of a sample of four Italian trawl fleets we developed a working model predicting fishing intensity (daily units of HP per unit area) from bathymetry, distance from port and fleet size (data sources and analysis details are found in the Supplementary Methods). This analysis only provided an approximate spatial picture of fishing effort. We omitted local scale predictors of fishing intensity such as avoidance of fisheries’ fleet size (data sources and analysis details are found in the Supplementary Methods).

We sampled four Italian trawl fleets we developed a working model predicting fishing intensity projected over the Adriatic. By using data on number, horse power (HP), and gross tonnage (GT) of boats fishing along the Adriatic coasts, we assumed that the intensity of fishing per unit of sea bed surface (at any point in the Adriatic Sea) was proportional to the cumulative effort exerted by all Adriatic fishing fleets, whose individual contribution depended on the distance between any point and the fleet harboring port, fleet size, and point bathymetry. Using empirical data of effort distribution of a sample of four Italian trawl fleets we developed a working model predicting fishing intensity (daily units of HP per unit area) from bathymetry, distance from port and fleet size (data sources and analysis details are found in the Supplementary Methods).

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Author contributions
F.F., G.C.O. and H.K.L. conceived and designed the study; F.F., G.C.O. and C.J.J. collected and analyzed the data; F.F., G.C.O., A.A.R. and H.K.L. wrote the manuscript.

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