2	Spatial heterogeneity in fishing creates de facto refugia for
3	endangered Celtic Sea elasmobranchs
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- 23 Abstract
- 24

25 The life history characteristics of some elasmobranchs make them particularly vulnerable to 26 fishing mortality; about a third of all species are listed by the IUCN as Threatened or Near 27 Threatened. Marine Protected Areas (MPAs) have been suggested as a tool for conservation 28 of elasmobranchs, but they are only likely to be effective if such populations respond to 29 fishing impact at spatial-scales corresponding to MPA size. Using the example of the Celtic Sea, we modelled elasmobranch biomass (kg h^{-1}) in fisheries-independent survey hauls as a 30 31 function of environmental variables and 'local' (within 20km radius) fishing effort (h v^{-1}) 32 recorded by Vessel Monitoring System (VMS). Model selection using AIC suggested 33 strongest support for linear mixed effects models including fishing effort, geographic location 34 and demersal fish assemblage. Each of these variables had approximately equal importance in 35 explaining elasmobranch biomass. Sampling sites in the lowest 10% of the observed fishing 36 effort range recorded 10 species of elasmobranch including the critically endangered Dipturus 37 spp. The most intensely fished 10% of sites had only three elasmobranch species, with two 38 IUCN listed as Least Concern. Our results suggest that spatial heterogeneity in fishing effort 39 creates de facto refugia for elasmobranchs in the Celtic Sea. However, changes in the present 40 fisheries management regime in the Celtic Sea could displace effort into these areas and 41 impair the refuge effect. 42

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46 1. INTRODUCTION

47

48	An emerging requirement of the Ecosystem Approach to Fisheries Management (EAFM) is to
49	understand the spatial scales at which the ecological impacts of fishing operate [1], [2]. Fish
50	communities typically are not homogeneous; structure and composition can vary in space as a
51	function of environmental variables such as habitat and benthic community composition [3],
52	[4], and these patterns of spatial variation can remain consistent over time [5]. Such
53	environmentally-driven spatial heterogeneity or 'patchiness' in the marine fish community
54	can be reflected in regional variation in size-structure [6]. However, statistical modelling of a
55	metric of size-structure and species composition (the Large Fish Indicator [7]) in the Celtic
56	Sea suggests that the fish community can also vary in space with 'local' (within 20-40km
57	radius) fishing intensity [8]. This fishing effect on spatial size-structure may occur because of
58	temporal stability in the regional distribution of fishing effort [9], [10] relative to environment
59	(e.g., substratum, [11]). Such stability may reveal time-lagged pressure-state relationships
60	between a local effort regime and the fish community it affects. In this context, fishing
61	impacts on the seabed (e.g., [12]) and on target communities [1], [13] can be spatially
62	discrete. Correct knowledge of such fishing impacts is critical to the use of spatial
63	management measures (e.g., Marine Protected Areas, MPAs) in conservation and recovery of
64	exploited marine communities [14].
65	
66	Fishing-induced curtailment of fish community size-structure (e.g., [15], [16]) reflects

67 changes in fish community species composition and evenness [17]. This change typically

68 comprises loss of larger body-sized species having life history traits including slow growth,

69 late age at maturity and low fecundity. These characteristics often render populations 70 particularly vulnerable to incidental [18] or target mortality [19], [20]. A group exemplifying 71 'slow' life history is the elasmobranchs, i.e., sharks, rays and chimaeras, which have among 72 the most complex reproductive strategies of all fishes [21]. In the North Atlantic, relatively 73 few elasmobranch species are targeted commercially (e.g., [22]), but many are known to be 74 vulnerable to fishing (e.g., [23], [24]). Some species of elasmobranchs may even have been 75 extirpated in heavily exploited regions, like the North Sea [25], [26]. In a specific example, 76 common skate Dipturus batis was already very rare in the Irish Sea by 1981 [27] and (now 77 classified as two separate species: Dipturus intermedia and D. flossada) has been listed by the 78 IUCN as Critically Endangered [28].

79

80 If fish community size-structure and species composition change in space with environment 81 and fishing intensity, then heterogeneity in distribution and abundance of certain vulnerable 82 elasmobranchs also can be expected. Such patchiness might create scope for informed spatial 83 management if areas of low fishing intensity act as refugia. Walker & Heessen [23] 84 speculated that since some areas in the North Sea are difficult to access with towed gear, such 85 areas could act as refugia for elasmobranch populations. There is evidence that formal MPAs 86 can contribute to conservation and management of elasmobranchs [29], [30] but this is 87 strongly contingent on movement patterns [31], which can vary with environmental 88 conditions [32]. Spatially discrete management of fishing effort could benefit fishes, 89 including elasmobranch species, whose abundance responded to 'local' fishing intensity at a 90 scale expedient to realistic (socio-economically acceptable) spatial management [33]. Some 91 modelling studies suggest that temperate MPAs should encompass around 80% of a species

92 range, and thus to be successful MPA size must increase with assumed species mobility [34]. 93 However, meta-analysis suggests that temperate marine reserves (<100km²) are associated 94 with positive responses in the abundance and biomass of some fish species, although often 95 this coincides with strong habitat association within the MPA boundary [35], [36]. Rogers et 96 al. [37] note that current elasmobranch abundance is lowest in the most heavily fished (south-97 eastern) part of the North Sea, although previously such species were common in this area 98 [38]. Greenstreet et al. [39] also observed that demersal fish species diversity has declined in 99 those areas of the North Sea showing greatest fishing effort, with the decline reflecting loss of 100 species such as the globally 'Vulnerable' (IUCN) spiny dogfish Squalus acanthius. These 101 observations also suggest some regional-scale response to fishing intensity. Given the critical 102 conservation status and growing public profile of elasmobranchs, it is important to understand 103 the spatial scale at which MPAs might be effective tools to conserve populations.

104

105 The Celtic Sea retains some of the largest remaining populations of many NE Atlantic 106 elasmobranch species [37], including the critically endangered D. intermedia and D. flossada. 107 In the current paper, we combined fisheries-independent survey data and fine-scale fishing 108 effort (Vessel Monitoring Systems, VMS) data from the Celtic Sea with several 109 environmental descriptors. The objective was to establish whether spatial heterogeneity in 110 fishing effort can lead to a temporally stable mosaic of fished and unfished areas that would 111 generate *de facto* refugia resulting in local changes in biomass and species composition of 112 elasmobranchs. De facto refugia (sensu [40]) are here considered to be areas where there are 113 no formal fishing restrictions but natural obstacles such as rough seabed or distance from port 114 that minimize actual fishing activity. Such refugia may be represent sites where establishment

115 of formal MPAs would result in minimal fishing effort displacement.

116

117 2. METHODS

118

119 In studies of spatial or temporal variation in fish abundance, standardised catch rate data (e.g.,

120 Catch Per Unit of Effort, CPUE) are often used. Standardised CPUE accounts for variation in

abundance due to environmental or other factors (see [41] for a review). In the current study,

122 linear mixed effects models that included environmental variables were used to test for an

123 effect of local fishing effort regime (hours fishing per year, h y⁻¹) on biomass of

124 elasmobranchs caught per hour of survey trawl sampling (kg h⁻¹) in the Celtic Sea.

125

126 Fishing effort data

127 International fishing effort was derived from Vessel Monitoring System (VMS) records

128 (2006-2011) for the area of the Celtic Sea within the Irish Exclusive Economic Zone (EEZ)

129 (Figure 1). VMS transmits the position and speed of fishing vessels at least every 2 hours. All

130 gears (otter and beam trawl and scallop dredges) were included and speed criteria were

applied to distinguish fishing activity from steaming and other non-fishing activity. Using

132 records from on-board observers, Gerritsen & Lordan [46] found that for otter bottom

trawlers, vessel speeds between 1.5 and 4.5 knots correctly identified fishing activity in 88%

134 of cases. Each VMS record where the vessels were deemed to be fishing was allocated an

135 effort value that was equal to the time interval between successive VMS records (generally 2

136 hours). For each IGFS sampling station, the value used for analysis was summed annual

fishing effort (h y⁻¹) within a 20km radius circle from the survey haul midpoint (Figure 1).
International VMS data were only available for survey stations within the Irish EEZ.
However, some circles extended outside this national boundary and/or onto land. In these
cases, effort was corrected for the area of each circle for which data were available by
dividing recorded values by the proportion of each circle comprising sea within the EEZ.
Only stations where >50% of the area of the 20km circle was sea and within the Irish EEZ
were used.

144

145 Ecological data

The Irish Groundfish Survey (IGFS) is a standardized bottom-trawl survey that includes the
Celtic Sea (Figure 1) and has occurred in late autumn since 1997. This survey is operated by
the Irish Marine Institute using a Grande Ouverture Verticale (GOV) trawl fitted with a 20mm
codend liner. Standard International Bottom Trawl Survey (IBTS) protocol is followed. In a
given year, trawl samples (approx. 30min duration) are collected at sites randomly selected
from a pool of around 100 fixed sampling stations ('Prime Stations'). All fish captured are
identified to species and measured (total length; L).

153

Using IGFS survey data (2006-2011), catch numbers at length were converted to weight (W) at length using weight at length relationships (W= αL^{β}), where the parameters α and β were obtained by direct analysis (common species) or from FishBase (www.fishbase.org). Catch weight at length of each demersal fish species and length class in each trawl sample (haul) were then converted to a density (kg h⁻¹) by dividing by the precise trawl duration.

Elasmobranch species richness (number of species) and biomass (kg h⁻¹) was then calculated
for each survey haul.

161

162 In any spatial investigation of the fish community it is necessary to account for biogeography 163 [37]. All stations were allocated to a Celtic Sea biogeographic sub-region based on 'similar' 164 [42] demersal fish species composition (henceforth 'fish assemblage region') (Figure 2). This 165 factorial variable (having four classes, East, Onshore, Midshore, Offshore) was derived from 166 root-transformed species abundance data from the IGFS. A resemblance matrix was generated 167 using the Bray-Curtis index of similarity, creating a dendrogram using the group-average 168 linkage clustering method and then followed by a SIMPROF test [42] to define clusters a 169 posteriori that were significantly (P<0.05) different [9]. In the study region (as in the North 170 Sea, [4], [5]) demersal fish assemblage was related to seabed substratum but may also 171 integrate the effects on fish community structure of associated oceanographic variables, 172 especially depth [43]. Each sampling station was also allocated to a substratum class (gravel, 173 sand or mud) using maps available on the Mapping European Seabed Habitats (MESH) 174 website (www.searchmesh.net). Because of differences in the fish community between the 175 shallower eastern area of the Celtic Sea and the deeper western shelf (e.g., [44], [45]), depth 176 (m) and location (Longitude + Latitude) were also modelled as candidate explanatory 177 variables of relative elasmobranch biomass. 178

179 Analysis

180 The effect of fishing effort (h y⁻¹) on elasmobranch biomass (kg h⁻¹) by survey haul was

181 estimated using models that accounted for environmental variables. Model selection was

182	conducted in an information theory context using AIC. The full starting model included: Fish
183	assemblage region, substratum, depth (m) and sampling location (Lat + Lon). A preliminary
184	comparison indicated that a linear model had a lower AIC than a non-linear GAM and hence
185	further analysis focused on linear models. Boxplots of model residuals showed variation in
186	elasmobranch biomass by Prime Station (Figure 3), and so a random effect of Prime Station
187	was included. In order to allow direct comparison of model coefficients, numerical variables
188	were standardised such that mean = 0 and variance = 1. The 'best' final model (lowest AIC)
189	had the following form:
190	
191	$Biomass_{ij} = \alpha + \beta_2 \times Effort_{ij} + \beta_3 \times Location_{ij} + \beta_4 \times Assemblage_{ij} + B_5 \times Effort_{ij} \times B_5 \times Effort_{ij} \times B_5 \times$
192	Assemblage _{<i>ij</i>} + a_i + ε_{ij}
193	
194	Where: Biomass _{<i>ij</i>} is elasmobranch biomass (kg h ⁻¹) for observation (haul) <i>j</i> at Prime Station <i>i</i>
195	and a_i is the random effect of Prime Station. Residual distributions suggested non-
196	heterogeneity so a structure was added that allowed variance to change with Location; this
197	resulted in acceptable residuals. A spline correlogram of model residuals against location (Lat
198	Lon) showed no spatial autocorrelation.
199	
200	This statistical modelling indicated a distinct area in the NE Celtic Sea where minimal fishing
201	effort was combined with greater biomass and species richness of elasmobranchs. We
202	hypothesised that this <i>de facto</i> refuge developed because fishermen avoid the area for one or
203	more of the following reasons:
204	

205	1. The catch (landings per unit effort, LPUE) of target species is relatively low in this area.
206	2. The relative cost of fishing this area, measured as distance from nearest port, is high.
207	3. The risk of losing gear due to rough ground is unacceptably high.
208	
209	Data were not available to support a robust quantitative analysis of this question, so a
210	qualitative approach was taken involving mapping and anecdotal knowledge.
211	
212	3. RESULTS
213	
214	Model coefficients indicated a negative effect of fishing effort on Celtic Sea elasmobranch
215	biomass. There was also an effect on elasmobranch biomass of fish assemblage region, and an
216	interaction between effort and assemblage region (Figure 4) with the strongest effort effect
217	across the 'East' region where greatest elasmobranch biomass was observed (Figure 5). In
218	addition, there was a positive effect on elasmobranch biomass of location (Lat + Lon), with
219	greatest biomass in the NE Celtic Sea. Fishing effort, location and fish assemblage region had
220	approximately equal importance as explanatory variables in the final model (Table 1).
221	
222	There was a distinct area in the NE Celtic Sea where low fishing effort overlapped closely
223	with greater elasmobranch biomass and species richness (Table 2; Figure 5). This area
224	showed moderate LPUE for commercial species, and was closer to port than other much more
225	heavily-fished areas of the Celtic Sea (Figure 5). However, fishermen have indicated that the
226	seabed in much of the area comprised highly dynamic sand features that made trawling
227	inefficient and unpredictable. We therefore suggest that hypothesis (3: risk of losing gear due

to rough ground) likely best explains the low effort area of the Celtic Sea that now representsa *de facto* elasmobranch refuge.

230

4. DISCUSSION

232

The spatial distribution of fishing effort is often very uneven [12] and can remain stable over time [10]. In the NE Celtic Sea (Figure 1), this creates areas where annual fishing effort within a 20km radius of IGFS survey sampling sites is consistently <3.0h km⁻². We find that these areas have many more elasmobranch species and greater elasmobranch biomass than geographically proximate heavily-fished areas. Our results suggest that heterogeneity in effort may create *de facto* refugia for Celtic Sea elasmobranchs, provided this mosaic of fishing effort distribution remains stable through time.

240

241 The distribution of elasmobranchs in the NE Atlantic shows broad patterns that are most 242 likely driven by environmental parameters at regional scales (100s km) [37]. Many 243 elasmobranch species also respond to local habitat characteristics such as substratum type 244 [47], [48] and depth [49], [50]. In this context, it might be suggested that remaining 245 (relatively) high biomass patches just reflect areas that had greatest elasmobranch biomass 246 prior to fishing. Depleted populations would likely contract spatially into to such optimal 247 areas [51]. However, we found that both fishing effort and habitat/environmental descriptors 248 were retained as important explanatory variables in models of elasmobranch biomass. This 249 suggests that *de facto* elasmobranch refugia may occur when low commercial fishing effort 250 overlaps with favourable habitat.

252	Anecdotal information suggested that shifting sandy seabed in parts of the refuge area makes
253	trawling difficult and hence uneconomic under the current management regime. The
254	environment may thus impart some degree of on-going natural protection from fishing.
255	However, some commercial fishing does occur in the area and LPUE can be quite high. This
256	existing effort means that changes in the fisheries management regime in the Celtic Sea (e.g.,
257	introduction of MPAs for other reasons) could displace effort into this area and perhaps
258	quickly impair its value as an elasmobranch refuge. Historical data (noted by [53]) on
259	fisheries discards of skates indicates that these species were previously abundant in areas
260	proximate to the Celtic Sea refuge, from where they have now been almost extirpated.
261	
262	Further work is required to understand how this <i>de facto</i> refuge functions to sustain
263	elasmobranch biomass and species richness. Protection of nursery areas has been considered
264	important in management of shark populations [54], [55]. Many shark species have distinct
265	nursery areas, typically in nearshore areas [56]. Juveniles are often sedentary [57] meaning
266	that they are likely to remain close to their natal area. Juveniles of Raja clavata can show
267	strong site fidelity [58], and Frisk et al. [59] found that enhanced juvenile survival could help
268	recovery of exploited skates. Notably, an analysis of long-term fisheries survey data (1967-
269	2002) around the British Isles identified the area of greatest elasmobranch biomass observed
270	in the current study as being important to juvenile Rajids and also found that juveniles of the
271	critically endangered D. Batis were only found in the Celtic Sea [60].
272	

273 In contrast, recent evidence suggests that protection of adults may be a more effective 274 elasmobranch conservation strategy than focusing on nursery grounds (see review in [55]). 275 This is because deterministic stock/recruitment relationships mean that the contribution of 276 juveniles to population growth rate is low compared to sub-adults and mature adults (e.g., 277 [21]). For example, modelling suggests that a 3-season closure would protect Thames Estuary 278 skate from fishing pressure, but predominately by conserving larger size-classes [61]. Adults 279 of some elasmobranch species, e.g. Dipturus batis, are highly sedentary [62] and don't move 280 out of low-effort areas where they receive some protection from fishing. Other ray 281 populations can also benefit from MPAs, although the effect varies with species life history 282 [63]. If protection of adult elasmobranchs is the optimal conservation strategy, then the 283 discovery of a Celtic Sea refuge for at least ten elasmobranch species becomes even more 284 important. Populations in this refuge, if protected, might act as a source that will help sustain 285 recruitment of these species in the Celtic Seas region.

286

287 The legal and management cost of establishing an MPA can be significant [64]. However, the 288 key restrictions on the success of MPAs include negative cultural [65], political [66] and 289 economic [67] impacts, and displacement of effort to other areas [68]. The Celtic Sea refuge 290 area currently identified consistently receives very little effort and hence these problems may 291 be limited as MPAs sited with reference to existing effort patterns are typically relatively 292 effective [33]. At the most pragmatic level, such an MPA would protect an area for which 293 survey data records greater elasmobranch abundance and species richness than anywhere else 294 in the region. Annual fisheries displacement by the MPA could be less than three hours per km^2 . 295

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568	ГАВ	LES

570	Table 1. Coefficients for models relating standardised elasmobranch biomass (kg h ⁻¹) in Celtic
571	Sea survey hauls to annual fishing effort (h y ⁻¹) (2006-2011) within 20km radius. Additional
572	variables are fish assemblage class (East, Inshore, Midshore, Offshore) and Location (Lat +
573	Lon).
574	
575	Table 2. Standardised biomass (kg h^{-1}) and species composition of elasmobranchs in survey
576	hauls (2006-2011) at sampling sites in the upper (High) and lower (Low) 10% of the observed
577	eastern Celtic Sea fishing effort (h y ⁻¹) range. IUCN status of each species is given.
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Variable	Value	SE	DF	t-value	p-value
Intercept	0.687	0.317	110	2.169	0.032
Fishing effort	-0.535	0.176	110	-3.046	0.003
Location	0.144	0.062	110	2.793	0.006
Inshore	-0.829	0.321	40	-2.582	0.014
Midshore	-0.974	0.331	40	-2.944	0.005
Offshore	-0.862	0.346	40	-2.491	0.017
Effort:Inshore	0.544	0.201	110	2.71	0.008
Effort:Midshore	0.431	0.184	110	2.342	0.021
Effort:offshore	0.669	0.181	110	3.69	< 0.001

591 Table 2.

Effort Category	IUCN	Biomass		
High			_	
Squalus acanthias	VU	2.63		
Mustelus asterias	LC	5.62		
Scyliorhinus canicula	LC	29.71	_	
Low				
Raja clavata	NT	4.94		Least Concern
Dipturus batis	CR	5.54	NT	Near Threatened
Scyliorhinus stellaris	NT	16.12	VU	Vulnerable
Mustelus asterias		16.65	EN	Endangered
Raja microocellata	NT	31.34	CR	Critically Endangered
Raja montagui		48.45		
Raja brachyura	NT	49.49		
Galeorhinus galeus	VU	87.55		
Squalus acanthias	VU	117.87		
Scyliorhinus canicula	LC	332.17		



Figure 1. Location of IGFS survey hauls in 2007 with associated 20km circles; other study
years have similar sample distribution. Fishing effort is shown as a background, where red is
highest and white is lowest effort. The border between UK and Irish Exclusive Economic
Zones (EEZ) is shown. ADD 2007 SAMPLING SITES (CURRENTLY 2008) AND ADD
EFFORT
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610 Figure 2. Environmental variables included in models of elasmobranch abundance in the

- 611 Celtic Sea: Depth, Location (Lat + Lon) and Fish assemblage region. ADD 2007
- 612 ASSEMBLAGE REGIONS (CURRENTLY 2008) AND ADD BATHYMETRY.



Figure 3. Boxplot of elasmobranch abundance by survey Prime Station. Values are residuals
from the 'best' (lowest AIC) linear model.



628 Figure 4. Main effects from a linear model of Celtic Sea elasmobranch abundance: Fishing

629 effort, Location (Lat + Lon), Fish assemblage region and fishing effort by assemblage region.



631 Figure 5. Landings Per Unit of Effort (LPUE) by Irish vessels (2006-2011). Locations of all

632 IGFS trawl samples used in the current study are shown. Standardised elasmobranch biomass

- 633 (kg h⁻¹) by sampling year is illustrated by the size of the bubbles. The legend shows reference
- 634 bubble sizes with associated biomass values. ADD MAIN FISHING PORTS