

1 SSG=see style guide

2 **Historical spatial reconstruction of a spawning-aggregation fishery**

3

4 Sarah M. Buckley^{1*}; Ruth H. Thurstan^{1,2}, Andrew Tobin³, John M. Pandolfi¹

5 ¹School of Biological Sciences, Gehrmann Building, The University of Queensland and

6 Australian Research Council Centre of Excellence for Coral Reef Studies, St Lucia,

7 Queensland 4071, Australia

8 ²Centre for Integrative Ecology, School Life and Environmental Science, Deakin

9 University, Burwood, Victoria 3125, Australia

10 ³Centre for Sustainable Tropical Fisheries and Aquaculture, School of Earth and

11 Environmental Sciences, James Cook University, Townsville, Queensland 4810, Australia

12 *mail s.buckley2@uq.edu.au

13 **Running head**

14 Spatial reconstruction of a spawning fishery

15 **Keywords**

16 Spatial reconstruction, fish-spawning aggregation, shifting baselines, commercial fishing,

17 historical ecology, Spanish mackerel, fishing power

18

19 **Abstract**

20 Aggregations of individual animals that form for breeding purposes are a critical ecological
21 process for many species, yet these aggregations are inherently vulnerable to exploitation .
22 Studies of the decline of exploited populations that form breeding aggregations tend to focus
23 on catch rate and thus often overlook reductions in geographic range. We tested the
24 hypothesis that catch rate and site occupancy of exploited fish-spawning aggregations
25 (FSAs) decline in synchrony over time. We used the Spanish mackerel (*Scomberomorus*
26 *commerson*) spawning-aggregation fishery in the Great Barrier Reef as a case study. Data
27 were compiled from historical newspaper archives, fisher knowledge, and contemporary
28 fishery logbooks to reconstruct catch rates and exploitation trends from the inception of the
29 fishery. Our fine-scale analysis of catch and effort data spanned 103 years (1911–2013) and
30 revealed a spatial expansion of fishing effort. Effort shifted offshore at a rate of 9.4 nm
31 /decade, and 2.9 newly targeted FSAs were reported/decade. Spatial expansion of effort
32 masked the sequential exploitation, commercial extinction, and loss of 70% of exploited
33 FSAs. After standardizing for improvements in technological innovations, average catch
34 rates declined by 90.5% from 1934 to 2011 (from 119.4 to 11.41 fish/vessel¹/trip). Mean catch
35 rate of Spanish mackerel and occupancy of exploited mackerel FSAs were not significantly
36 related. Our study revealed a special kind of shifting spatial baseline in which a contraction
37 in exploited FSAs occurred undetected. Knowledge of temporally and spatially explicit
38 information on FSAs can be relevant for the conservation and management of FSA species.
39

40 **Introduction**

41 Mass aggregations of individuals for the purpose of breeding, migrating, feeding, or birthing
42 in terrestrial and marine ecosystems are well known. Aggregation events that occur at
43 predictable times and in a few restricted locations make the animals acting in these events
44 highly vulnerable to exploitation (Bauer and Hoye 2014). Long-term declines in abundance
45 of aggregating terrestrial species that are widespread, such as wildebeest (*Connochaetes*), are
46 generally accompanied by a similar decline in the number of sites occupied (i.e., occupancy)
47 by aggregations as a result of hunting and habitat loss (Laliberte & Ripple 2004). Similar
48 long-term declines in the abundance and distribution of marine species that form
49 aggregations have been documented (e.g. McClenachan & Cooper 2008). However, changes
50 in the occupancy, in particular the breeding component, of fish populations that form
51 spawning aggregations are rarely quantified. Accounting for fine-scale spatial changes in a
52 widespread species is important because the decline and extirpation of the breeding
53 component can disrupt reproductive behavior, reduce genetic diversity, and compromise the
54 ability of a population to withstand future threats (Ciannelli et al. 2013). Quantifying
55 spatiotemporal changes in the abundance and geographic distribution of a population can
56 facilitate an accurate assessment of a species conservation status and help set effective
57 recovery targets.

58 The vulnerability of exploited fish-spawning aggregations (FSAs) is evident from the severe
59 and rapid declines in abundance of numerous species across a range of families (Sadovy de
60 Mitcheson and Erisman 2012). Examples of recognized losses of FSAs include the tropical
61 Nassau grouper (*Epinephelus striatus*), which once formed multiple FSAs throughout the
62 entire Caribbean (Sadovy and Eklund 1999), and the long-lived deepwater orange roughy
63 (*Hoplostethus atlanticus*), whose population collapsed within a decade of the onset of
64 exploitation (Clark 2001). Spawning aggregations are particularly vulnerable to overfishing

65 occurring undetected due to hyperstability. Hyperstability occurs when high catch rates are
66 maintained while fishers sequentially deplete or extirpate aggregations, resulting in the
67 sudden collapse of exploited populations (Sadovy de Mitcheson and Colin 2012).

68

69 One of the most documented relationships in macroecology is the abundance–occupancy
70 relationship (AOR) (Gaston et al. 2000). A positive relationship between population
71 abundance and occupancy is predominant within (intraspecific) and among (interspecific)
72 terrestrial and marine taxa (Blackburn et al. 2006; Borregaard and Rahbek 2010). This
73 relationship extends to exploited marine fishes (Fisher and Frank 2004; Webb et al. 2011).
74 However, for highly aggregated species, a positive AOR is less likely. Instead, they may
75 exhibit a nonsignificant or negative AOR (very high abundance of individuals occur in a few
76 sites), although this has rarely been quantified (Webb et al. 2012).

77

78 Reconstructions of the size of breeding populations that form FSAs are often deduced from
79 landings collected at the fishery level (Sadovy de Mitcheson et al. 2008). However, due to
80 hyperstability in species that aggregate when they spawn, catch data alone do not accurately
81 reflect the abundance changes in the breeding population (Erisman et al. 2011). We devised
82 an alternative approach to estimate abundance of aggregating species for which reliable data
83 are lacking. Specifically, we sought to quantify the geographic changes in fishery targeting
84 of FSAs and catch rate over time.

85

86 Spanish mackerel (*Scomberomorus commerson*) sustains local commercial, recreational,
87 and artisanal fisheries throughout its Indo-Pacific distribution (Juan-Jordá et al. 2011).
88 Where stock assessments exist (Southern Arabian Gulf and Oman), generally, the fisheries
89 are fully exploited (i.e., a stock is fished to the maximum and an increase leads to

90 overfishing) or overfished, likely due to the predictable aggregating behavior exhibited
91 during spawning, feeding, and migrating (Grandcourt 2005; Govender et al. 2006). In some
92 cases, overfishing has caused steep declines in mackerel biomass and collapse of the fishery
93 (Collette et al. 2011). A few studies have provided evidence of recovery of taxa within the
94 scombrids (Juan-Jordá et al. 2011). However, these assessments do not provide a specific
95 analysis of the history of the fishery or of the exploitation of the FSAs of Spanish mackerel
96 populations.

97

98 We reconstructed the catch rate and history of occurrence of exploited FSAs of a commercial
99 fishery that has targeted the Spanish mackerel within the Great Barrier Reef (GBR) for over
100 a century (McPherson 1985). Spanish mackerel is a pelagic predator that exhibits site fidelity
101 by migrating long distances to a few discrete breeding sites in the central GBR, forming
102 FSAs between October and November each year (Tobin et al. 2014). These FSAs form part
103 of a commercial fishery that targets Spanish mackerel along the east coast of Australia,
104 termed the east coast Spanish mackerel (ECSM) fishery. Despite the limited spatial extent of
105 the FSAs, which are restricted to a small number of reefs within the GBR, the landings from
106 these aggregations represent a disproportionately large component of the total annual catch
107 of the ECSM fishery (Tobin et al. 2013).

108

109 Concerns have been raised regarding the vulnerability of the GBR Spanish mackerel to
110 decline due to its transient aggregating behavior and the sustainability of the commercial
111 fishery (McPherson 2007; Tobin et al. 2013). The most recent stock assessment shows that
112 the current stock biomass ranges between 39–51%, which is within the range of maximum
113 sustainable yield (approximately 50%) and maximum economic yield (approximately 40%)
114 (Campbell et al. 2012). However, the 95% confidence intervals show current biomass could

115 be as low as 34%. Hence, Spanish mackerel could be overfished because the biomass may be
116 <40%. There are a number of uncertainties surrounding the stock assessment due to data
117 quality (a lack of fishing effort time and zero catch records) and accounting for
118 hyperstability of the aggregating species.

119

120 We sought to determine the trajectory of both the catch rate and occupancy of the Spanish
121 mackerel FSAs and whether a relationship between the 2 exists. Occupancy was estimated as
122 the proportion of FSAs (total number of fished FSA sites/total number of known FSA sites)
123 per decade. We hypothesized that catch rate and occurrence of exploited FSAs decline over
124 time and the relationship between catch rate and occupancy over time is negative or
125 nonsignificant. We extracted and combined data from historical newspapers, fisher
126 knowledge, and commercial logbook records to reconstruct spatially explicit catch and effort
127 trends for the Spanish mackerel commercial fishery. We evaluated two factors critical for
128 assessing temporal trends in commercial catch: changes in recalled catch rate at a fishery
129 (Townsville and Cairns) scale and catch rates from the contemporary Townsville fishery
130 standardized for improvements in gear and technology.

131 **Methods**

132 *Data review*

133 We compiled data on catch rate, the geographic distribution of fishing effort, and temporal
134 changes in fishing power (i.e., the efficiency of an average vessel at catching Spanish
135 mackerel) in the spawning fishery from historical archives (1911–1980), fisher interviews
136 (1948–2013), and contemporary commercial fisheries logbooks (1990–2011).

137 We searched newspaper records archived by the National Library of Australia and the State
138 Library of Queensland for references relating to the GBR FSA fishery. Metropolitan
139 newspapers were examined in digital archives (1803 -1954) and hard copies of regional
140 newspapers were searched (National Library of Australia 2014). For the digital archives,
141 standardized searches were conducted using the key phrases *Spanish mackerel spawning* and
142 *Spanish mackerel catch*. During the early period of the fishery, Spanish mackerel were
143 referred to as kingfish and snook, and these terms were included in our search. We extracted
144 all quantitative information specific to the FSA fishery (i.e., weight landed (8 kg = 1 fish),
145 date landed, vessel) from the historical archives to construct catch rates, which we calculated
146 as the number of Spanish mackerel fishing vessels per trip. We also gathered descriptions of
147 fishing gear and technology, fishing location, fishing effort, and perceptions of the fishery
148 (Supporting Information). Other historical sources were investigated for spawning-specific
149 data, including the annual reports of the Queensland Marine Department (1901 to 1935) and
150 Queensland Fish Board records (1946 -1981).

151

152 To gather catch and effort data we conducted semi structured interviews with 47 commercial
153 fishers who had fished the SAF. We interviewed fishers living along the east coast of
154 Queensland and covered a distance of 1500 km (Fig. 1). Participants were selected by
155 snowball sampling (i.e., fishers were recruited by interviewee referral). This method ensured
156 that we sampled expert SAF fishers (i.e., those with a minimum of ten years fishing
157 experience targeting the SAF). Our research protocol was approved by from the University
158 of Queensland Ethics Committee and informed consent was obtained from all fishers. All
159 interviews were conducted individually and lasted from 1.5 to 5 hours.

160

161 To verify whether fishers recalled the exploitation of FSAs rather than exploitation of fish

162 schooling, we asked them how they knew the fish were spawning. To be included in the
163 study, fishers had to report one of the defined criteria that represented direct or indirect
164 indicators of a spawning aggregation (Domeier 2012). Direct indicators included gamete
165 release in the water and multiple gravid females. Indirect indicators included the density of
166 fish being 3 times or more of the non spawning density or catch rates, high gonadosomatic
167 index, courtship, and coloration changes exclusively associated with spawning (Sadovy
168 2003).

169

170 We gathered records of FSA site names, number of hours spent fishing, and fishing effort
171 (number of vessels fishing per operation, total number of vessels in the fleet, and distance
172 traveled offshore) for both the beginning and end or the most recent period of each fisher's
173 career. We also recorded the timing and rate of adoption of each gear and technology used
174 (global positioning systems [GPS], color depth sounders, paravanes [device that allows baited
175 hooks to be trolled deep in the water column] throughout their fishing careers (O'Neill et al.
176 2003). In the final part of the interview, we asked fishers to recall good, average, and poor
177 catch rates (numbers of fish caught per hour) during the past year or when they last fished,
178 when they first fished, and any other periods they recalled (Daw et al. 2011). We
179 reconstructed time series of spatially explicit catch rate from fishers' perceptions (1940-
180 2013). Many fishers recalled good, average, and poor catches from more than one period for
181 a specific region (Townsville or Cairns). Finally, 42 recreational fishers were asked whether
182 they had recently sighted Spanish mackerel in the former FSA sites.

183

184 Commercial daily-logbook catch data for the FSA fishery from 1990 to 2011 were acquired
185 from the Queensland Department of Agriculture, Fisheries and Forestry. The data consisted
186 of the daily catch of each operation, defined as an unknown number of vessels catching fish

187 under one license. We used a spatial resolution of 30 x 30 minutes (latitudinal and
188 longitudinal grids) for recorded catches and extracted catch landings for the spawning
189 months (October and November) from the Townsville FSA fishery region. A bias that may
190 occur within newspaper articles is the reporting of only the best catches. To improve
191 comparability of catches between the historical newspapers and contemporary commercial
192 logbooks, we ranked the catch of the fishers from the commercial logbooks and compared
193 newspaper reports with reports of the 10 fishers with the highest average landings.
194

195 *Calculating spatial distribution of fishing effort*

196 We spatially partitioned data on commercial fishing effort to determine fine-scale changes in
197 exploitation patterns of the GBR FSA fisheries. To do so, we gathered details of fishing
198 locations and descriptions of grounds from both interviews and historical archives
199 (Supporting Information). We summed the total number of exploited FSAs from fishers and
200 newspapers during the spawning season per decade. Unfished FSAs were also included in
201 our analyses – these were observed FSAs that were previously fished but are now situated in
202 marine protected areas. The distance traveled from the home port to the farthest offshore
203 FSA sites each decade was calculated and defined as the total distance traveled offshore.
204 This enabled us to estimate fisher movement per decade from 1910 to 2010.
205

206 *Testing accuracy of recalled catch rates*

207 To investigate the accuracy of recalled catch rate, we used Daw et al.'s (2011) approach. We
208 compared the memory of 10 fishers' catch rates (good, average, poor) with fishers' recorded
209 catch for the corresponding period. We extracted all recorded catches from fishers' personal
210 logbooks, calculated the mean, and ranked all logged catches for the same period that fishers

211 recalled catches. We determined whether the variability of recalled catch fell within the
212 distribution of recorded catches for each fisher.

213

214 *Estimating catch rate and effort trends over time*

215 We used linear mixed-effects (LME) models to examine the temporal changes in catch rate
216 over time and the effects of the form of data on temporal trends. The nested structure called
217 for a linear mixed-effect model to account for fisher identity, where individual fishers
218 reported multiple observations of catches for more than one period of time. The random
219 structure allowed the intercept and slope to vary randomly with interviewees in each model.
220 Analyses were implemented using the lmer function in R lme4 package (Bates et al. 2013).
221 The maximum-likelihood estimation and model validation were carried out by plotting
222 standardized residuals against fitted values to identify violations of homogeneity. Data were
223 log transformed to meet assumptions of homoscedasticity.

224

225 First, we used LME models to test whether the different types of catch rates (good, average,
226 and poor) of exploited FSAs recalled by fishers changed significantly over time. The catch
227 rates may not be entirely independent of each other, but given the potentially broad period of
228 time (a year or more) that a fisher was being asked to recall catches, they were unlikely to be
229 recalling a poor, average, and good catch from a specific trip. Hence, these different types of
230 catch rates were treated as independent for the purpose of the analysis. In LME models 1-3
231 the number of fish per fisher per hour was a response variable, decade was a fixed factor,
232 and fisher identity was a random effect for good, average, and poor daily catch respectively.

233

234 Second, we explored the effect of increasing fishing power by comparing the mean catch rate
235 per year of the historical catch per unit effort (CPUE) and both the contemporary $CPUE_{raw}$

236 and contemporary $CPUE_{adjusted}$ (where catch rate was adjusted for changes in fishing power
237 over time). First a fishing power index was constructed. The four most influential fishing
238 operation characteristics (number of vessels per fishing operation, paravanes, colour sounders
239 and GPS) as perceived by fishers were used to account for the effect of increasing fishing
240 power on the catch rate. Ten of the interviewed fishers provided estimates of the proportional
241 increase in fishing efficiency as a result of adopting each new fleet characteristic. Only data
242 from fishers who had been operating prior to adopting the new technology were used and
243 averaged these across the number of fishers. For each characteristic, the average percentage
244 increase in catch by fishers employing the new characteristic was multiplied by the
245 percentage of the fleet employing that technology per year (Marriott et al. 2011). The
246 percentage increase of all the fleet characteristics was combined to provide annual estimates
247 of overall change in the fishing power index (baseline value; 1 and upper value; 3.5).

248

249 The magnitude of the increasing fishing power effect on the modern catch time series data
250 was explored by comparing the modern catch time series with modern catch time series
251 accounting for fishing power. Two alternative models with the same fixed-effects structures
252 but different assumptions about the random-effects structure were fitted to the data: no
253 random effects and random fisher identity effect. We used the Akaike information criterion
254 (Akaike 1974) to compare the null and full models. Maximal LME models were used for
255 further inference (Barr et al. 2015). In LME models 4-6, mean number of fishing trips per
256 year was a response variable, year was a fixed factor, and fisher identity was a random effect
257 for historical $CPUE$, contemporary $CPUE_{raw}$, and contemporary $CPUE_{adjusted}$ respectively.

258

259 *Investigating the abundance-occupancy relationship*

260 We investigated the intraspecific abundance-occupancy relationship (AOR) of the Spanish
261 mackerel FSA at a decadal scale (1940 and 2010). Abundance was measured as the mean
262 catch rate of Spanish mackerel within fished FSAs per decade. Occupancy was estimated as
263 the proportion of FSAs (total number of fished FSA sites/total number of known FSA sites)
264 per decade. We used a log linear model to examine the relationship between catch rates and
265 occupancy (Webb et al. 2007) using standard least squares with the lm function for each
266 decade. Spearman's rank-correlation coefficients between time and abundance and the
267 correlation of occupancy and time were estimated (Fisher and Frank 2004) to determine
268 whether one or both of these variables were associated with the strength and form of the
269 intraspecific relationship.

270 **Results**

271 *Historical expansion and contraction of exploited FSAs*

272 Commercial fishing of FSAs commenced in the inshore grounds off Townsville in 1911
273 (Townsville Daily Bulletin 1934). Reports from newspaper archives indicated a rapidly
274 increasing fleet depleted inshore FSAs within three decades (1911-1941). During this time,
275 fishers increased the total distance traveled offshore by an order of magnitude, from 5 to 51.4
276 nm (Fig. 2a & b; Supporting Information). Fisher interviews revealed that after 1940 the
277 Townsville FSA fishery continued to shift offshore, increasing its range to both the north and
278 south. By 2000 the fishery had contracted and today remains completely offshore. In
279 contrast, exploitation of the Cairns FSA fishery showed a pattern of discovery, expansion,
280 contraction, and collapse within four decades (1950-1990; Fig. 2a). From the early 1980s,
281 fishers began exiting the Cairns fishery, and by 1995 the entire Cairns FSA fishery fleet had
282 either exited the fishery or displaced effort to the offshore spawning grounds off Townsville.

283 A gradual increase in the total number of FSAs exploited was observed during the early
284 period (1911-1949) of the spawning fishery in the GBR. From 1950 to 1990, the total
285 number of FSAs exploited per decade increased from 10 to 23. From 1910-1990, the total
286 distance traveled offshore rose from 5 to 80 nm (Fig. 2b,c), an expansion rate of 9.4 nm/
287 decade. By 2000 the total number of FSAs exploited on the GBR was reduced to 30% of the
288 total number of exploited FSAs (Fig. 2c). No recreational fishers ($n=42$) had fished or
289 sighted an inshore Townsville or Cairns FSA in the past 20 years.

290 *Declines in perceived, good, average, and poor catch rates*

291 In our interviews, fishers recalled catch rates that supported the decline in the targeting of
292 FSAs of the Cairns and Townsville fisheries. A substantial declining trend was observed in
293 all the catch rate types recalled by fishers for each fishery (Fig. 3). The good and average (but
294 not poor) catch rates reported by Cairns fishers showed a significant decline from 1970 to
295 1990 (LME1 good $n=24$, $F_{1,18} = 6.740$, $p = 0.047$; LME2 average $n=25$, $F_{1,18} = 9.593$, $p =$
296 0.012) (Fig. 3a & Supporting Information). The Cairns catch-rate reduction was so large by
297 1995 all fishers had either exited the fishery or shifted effort to the Townsville fishery (Fig.
298 3a). Similarly, Townsville catch rates observed by fishers exhibited significant declines, with
299 the exception of good catch, which remained stable over time (LME2 average $n=107$, $F_{1,105} =$
300 14.03 , $p = 0.017$; LME3 poor $n=107$, $F_{1,105} = 19.82$, $p < 0.001$; (Fig. 3b & Supporting
301 Information). Despite an 87% decline in the Townsville fleet size by 2000, there were no
302 more new FSAs to exploit, so catch rates continued to decline for the Townsville fishery (Fig.
303 3; Supporting Information).

304

305 *Relationship between catch rate and occurrence of exploited FSAs*

306 Mean catch rate and occurrence of exploited FSAs were not related ($r = -0.294$, $p =$
307 0.479 ; Fig. 4a). Of the temporal correlations, Spearman's rank correlation coefficient showed

308 a significant negative ($r = -0.321$, $p < 0.001$; Fig. 4b) trend between catch rate and time. We
309 also found a negative but nonsignificant ($r = -0.418$, $p = 0.173$; Fig. 4c) temporal change in
310 the occurrence of exploited FSAs.

311

312 *Standardized catch rate and historical baseline*

313 Between 1934 and 1947, newspaper articles provided 304 quantitative records of historical
314 catch from 159 vessels. Although the annual average catch rate for Spanish mackerel was
315 highly variable during the historical period, no statistically significant time-series trend was
316 observed (Fig. 5a [LME4], Table 1, Supporting Information). Notable advancements in
317 fishing power commenced following World War II; the mean number of dory vessels fishing
318 per operator increased (Fig. 5b). Fishers quantified this operational variable as the most
319 influential in that it inflated the catch rate by 93.8% (Supporting Information). Peak fishing
320 efficiency in the mid-1980s coincided with the adoption of GPS and color sounders, but
321 efficiency declined after 1990 as the number of vessels fished by a single operator decreased
322 (Fig. 5b; Supporting Information). Mean contemporary catch rate differed significantly when
323 the contemporary CPUE_{raw} was adjusted using the fishing power index from fisher
324 perceptions. Prior to adjusting for fishing power, mean contemporary catch rate was 21.74
325 (95% CI 21.11–22.37) fish/operation/trip (95% CI 10.78–12.04) reducing to 11.41
326 fish/vessel/trip (95% CI 10.78–12.04) after adjustment (Figure 5a [LME5 and LME6], Table
327 1, Supporting Information). Despite the use of only the top 10 fishers' catches (which
328 minimizes estimated declines relative to those based on all fishers' catches), a significant
329 difference between the historic and modern period was observed. The mean catch rate of
330 Spanish mackerel decreased to 9.5% of the historical catch rate, from 119.79 (95%
331 confidence interval, 110.22–129.35) to 11.41 (95% confidence interval, 10.78–12.04)
332 fish/vessel/trip.

333 **Discussion**

334 Conservation of a transient aggregating species is intrinsically linked to the effective
335 management of FSAs (Sadovy de Mitcheson et al. 2008; Erisman et al. 2015). For species
336 with FSAs that are affected by anthropogenic activities, such as exploitation, understanding
337 the complete historical perspective of exploitation can contextualize the current status of a
338 fishery (e.g. Cardinale et al. 2011). In our historical approach, we examined long-term trends
339 and the relationship between the catch rate and occupancy of FSAs for the Spanish mackerel
340 FSA fishery from 1911 to 2013. We found a significant decline in both the catch rates and
341 occurrence of exploited FSAs. We observed a loss of exploited FSAs and an offshore shift in
342 exploration of additional FSAs within 2 decades of initial commercial exploitation of the
343 Townsville fishery, as well as the commercial extinction of FSAs in the Cairns fishery, when
344 the catch rate decreased to a point where fishing was no longer economically viable and
345 fishers stopped fishing in those grounds (Safina 1994). The spatial pattern exhibited by
346 Spanish mackerel is consistent with the serial depletion and collapse of FSA fisheries (e.g.
347 Clark 2001), and fishers' lack of awareness of former FSAs can be identified as shifting
348 baselines. We suggest that in the century since fishing began, the lack of spatial data on
349 exploited FSAs and spawning catch data prior to 1988 has contributed to shifting baselines.

350

351 We found a 90.5% decline in catch rates from the Townsville FSA fishery from 1934 to
352 2011, despite a significant decline in the total fleet effort in the contemporary fishery. Fisher
353 observations provided new insights into the catch trends and occurrence of a second,
354 unrecorded spawning fishery, in Cairns, located within the ECSM. The declining catch trends
355 observed within the Cairns fishery were steeper than for the Townsville fishery despite
356 similar improvements in gear and technology and spatial expansion of exploited FSAs. We
357 suggest that the FSAs supporting the fishery have died out because recreational fishers who

358 still target Spanish mackerel within the areas where Spanish mackerel FSAs once formed
359 since 1980 stated that they have not sighted any Spanish mackerel FSAs. The decline in catch
360 rate and exploited FSAs can probably be extrapolated to mean the loss of some of the local
361 spawning population because the commercial fishers target both aggregations before
362 spawning and spawning FSAs (Tobin et al. 2014).

363

364 Abundance-occupancy relationships are typically positive (Blackburn et al. 2006), but we
365 hypothesized that the AOR for a species that exhibits highly aggregated behavior is negative
366 or nonsignificant. We found a nonsignificant, albeit slightly negative, trend. Overall, the local
367 catch rate decreased by 90.5%, and occupancy mirrored that decline. However, we propose
368 that the nonsignificant trend observed over time was due to only a small proportion of FSAs
369 being exploited in the earliest three decades; the number of fished FSAs expanded and then
370 contracted sharply (by 70%) within two decades.

371

372 Historical data are subject to many problems, and their potential biases must be examined if
373 the data set is to be used as a reference point for past fisheries productivity. The main issues
374 for our findings were that the data were derived from disparate data sources, and each data
375 type had inherent biases, which could result in incomplete time series and uncertainty in
376 analytical robustness. The significant difference between the historic and modern catch rates
377 must be interpreted with caution because the time series of catch rate were incomplete. No
378 other data sources were available from that period to compare and determine the reliability of
379 the catch rate data. Despite these caveats, newspaper data were numerous and were
380 considered representative of the historical period due to the variability in catches landed by
381 vessels within one spawning season and newspaper articles described landings from multiple
382 vessels as good, average, or poor.

383 Commercial logbook data were plentiful but represented a small sample size (the top ten
384 fishers with the highest catch rates) of the current fisher population. Furthermore, we
385 accounted for only the top four gear and technology options adopted by fishers. This could
386 have led to an overestimated catch rate in the modern period; hence, our modern, adjusted
387 data are likely conservative. Fishers stated that the total number of hours fished increased per
388 day throughout their fishing careers, so we did not account for the effect of fishers taking
389 longer to catch fish. Our comparison of fishers' recalled catch rates (good, average, and poor)
390 were observed within the distribution of recorded logbook catches. Hence, we considered
391 fishers' perceptions of catch trends reliable.

392 Previous studies show that the collection of data during the development of the fishery can
393 extend the time series relevant for models and reduce the influence of changing baselines
394 (e.g. Engelhard et al. 2015). Quantifying and accounting for key parameters, such as
395 historical changes in fishing effort, fishing efficiency, and spatial changes, could be used in
396 stock assessments to reconstruct catch rates with greater certainty (Hilborn and Walters
397 1992). However, historical data sources are challenging to incorporate into stock assessment
398 due to their respective biases, including incomplete data, bias in reporting of data, and the
399 temporal and spatial scale of data.

400

401 Raising awareness of the spatial loss of FSAs occurring undetected may encourage
402 communication between fisheries and conservation management (Erisman et al. 2015). Both
403 fisheries and conservation management consider FSAs a priority to manage but for different
404 purposes. For example the objective of managing FSAs for Queensland fisheries management
405 is the sustainable exploitation of the stock while for the Great Barrier Reef Marine Park
406 Authority (conservation management) the goal is to ensure decreases and local extinctions of
407 FSAs within the GBR are minimized or do not occur at all (Russell and Pears 2008;

408 Campbell et al. 2012). Thus, the decline in FSAs represents a focal point for both
409 conservation and sustainable management (Erisman et al. 2015).
410
411 Shifting spatial baselines represent a state where the decline in geographic extent has been
412 lost to human memory. We suggest that a lack of historical data, sequential exploitation, and
413 increases in fishing power in the GBR spawning fishery have contributed to resource users
414 and management not incorporating the past distribution and abundance of this species into
415 conservation frameworks. Despite concerns and research conducted in the earlier decades of
416 exploitation of the ECSM FSAs (Munro 1942), no management mitigation has occurred that
417 explicitly addresses the loss of Spanish mackerel FSAs. Furthermore, at present empirical
418 data are lacking to test the effectiveness of this specific management measure to protect
419 FSAs of Spanish mackerel (Tobin et al. 2014). We believe that documenting historical
420 spatial baselines improves our perceptions of, and expectations for, breeding aggregations
421 and the overall population size of aggregating species (Cardinale et al. 2011) and creates an
422 enhanced framework for setting conservation targets.

423 **Acknowledgments**

424 We especially thank to all the Spanish mackerel fishers who not only provided the data used
425 here but also shared their memories, photographs, and time with us. We thank Queensland
426 Fisheries for access to contemporary catch rate data and L. McClenachan of Colby
427 University, D. Cameron of the Great Barrier Reef Marine Park Authority, L. Litherland, and
428 the UQ Marine Palaeoecology lab members for their comments on the manuscript. P.
429 Rachello-Dolmen assisted in constructing the ARC GIS figures. The manuscript was
430 considerably improved by comments from 4 anonymous reviewers, 1 anonymous editor, and
431 the regional editor E. Johnston. S.B., R.T., and J.P. were supported by the Australian
432 Research Council (ARC) Centre of Excellence for Coral Reef Studies and the Fisheries

433 Research and Development Corporation (project 2013-018). A.T. and S.B. were supported
434 by funding from the Fisheries Research Development Corporation (project 2010-007) on
435 behalf of the Australian Government.

436

437 **Supporting Information**

438 Examples of data sourced from newspaper archives (Appendix S1), estimates of fishing
439 power (Appendix S2), linear mixed-effect results of recalled catch (Appendix S3),
440 comparison of recalled and recorded catches (Appendix S4), trends in fleet size and gear and
441 technology (Appendix S5), and diagnostic statistics for linear mixed effects with a random
442 effect structure (Appendix S6) are available online. The authors are responsible for the
443 content and functionality of these materials. Queries (other than absence of the material)
444 should be directed to the corresponding authors.

445 **Literature Cited**

446 Akaike H. 1974. A new look at the statistical model identification. *IEEE Transactions on*
447 *Automatic Control* **19**:716–723.

448 Barr DJ, Levy R, Scheepers C, Tily HJ. 2013 Random effects structure for confirmatory
449 hypothesis testing: Keep it maximal. *Journal of Memory and Language* **68**: 255-278.

450 Bates D, Maechler M, Bolker B, Walker S. 2013. lme4: linear mixed-effects models using
451 Eigen and S4 classes. <https://cran.r-project.org/web/packages/lme4/> (accessed March 2016).

452 Blackburn TM, Cassey P, Gaston KJ. 2006. Variations on a theme: sources of heterogeneity
453 in the form of the interspecific relationship between abundance and distribution. *Journal of*
454 *Animal Ecology* **75**: 1426–1439.

455 Borregaard MK, Rahbek C. 2010. Causality of the relationship between geographic
456 distribution and species abundance. *Quarterly Review of Biology* **85**: 3–25.

457 Bauer S, Hoyer BJ. 2014. Migratory animals couple biodiversity and ecosystem functioning

458 worldwide. *Science* **344**:e1242552.

459 Campbell AB, O'Neill MF, Staunton-Smith J, Atfield J, Kirkwood J. 2012. Stock assessment
460 of the Australian East Coast Spanish mackerel (*Scomberomorus commerson*) fishery.
461 Department of Employment, Economic Development and Innovation, Queensland
462 Government, Brisbane, Queensland.

463 Cardinale M, Bartolino V, Llope M, Malorano L, Skoid M, Hagberg J. 2011. Historical
464 spatial baselines in conservation and management of marine resources. *Fish and Fisheries*
465 **108**:289–298.

466 Ciannelli L, Fisher J, Skern-Mauritzen M, Hunsicker ME, Hidalgo M, Frank KT, and Bailey
467 KM. 2013. Theory, consequences and evidence of eroding population spatial structure in
468 harvested marine fishes: a review. *Marine Ecology Progress Series* **480**:227–243.

469 Clark M. 2001. Are deepwater fisheries sustainable? The example of orange roughy
470 (*Hoplostethus atlanticus*) in New Zealand. *Fisheries Research* **51**:123–135.

471 Collette BB, Chang SK, Di Natale A, Fox W, Juan-Jorda M, Miyabe N, Nelson R. 2011.
472 *Scomberomorus commerson*. The IUCN Red List of Threatened Species. Available from
473 <http://www.iucnredlist.org/details/170316/0> (accessed July 2014).

474 Daw TM, Robinson J, Graham NAJ. 2011. Perceptions of trends in Seychelles artisanal trap
475 fisheries: comparing catch monitoring, underwater visual census and fishers' knowledge.
476 *Environmental Conservation* **38**:75–88.

477 Domeier ML. 2012. *Revisiting Spawning Aggregations: Definitions and challenges. Pages 1-*
478 *20. Reef Fish Spawning Aggregations: Biology, Research and Management.* Fish & Fisheries
479 Series Volume 35.

480 Engelhard, G.H., Thurstan, R.H., MacKenzie, B.R., et al. (2015) ICES meets marine
481 historical ecology: placing the history of fish and fisheries in current policy context. *ICES*
482 *Journal of Marine Science* **73**: 1386-1403.

483 Erisman BE, Allen LG, Claisse JT, Pondella II DJ, Miller EF, Murray JH, Walters C. 2011.
484 The illusion of plenty: hyperstability masks collapses in two recreational fisheries that target
485 fish spawning aggregations. *Canadian Journal of Fisheries and Aquatic Sciences* **68**:1705–
486 1716.

487 Erisman BE, Heyman WD, Kobara S, Ezer T, Pittman S, Aburto-Oropeza O, Nemeth RS.
488 2015. Fish spawning aggregations: where well-placed management actions can yield big
489 benefits for fisheries and conservation. *Fish and Fisheries* **18**: 128-144.

490 Fisher JAD, Frank KT. 2004. Abundance-distribution relationships and conservation of
491 exploited marine fishes. *Marine Ecology Progress Series* **279**: 201–213.

492 Gaston KJ, Blackburn TM, Greenwood JJD, Gregory RD, Quinn RM, Lawton JH. 2000.
493 Abundance-occupancy relationships. *Journal of Applied Ecology* **37**: 39–59.

494 Govender A, Al-Oufi H, McIlwain JL, Claereboudt MC. 2006. A per-recruit assessment of
495 the kingfish (*Scomberomorus commerson*) resource of Oman with an evaluation of the
496 effectiveness of some management regulations. *Fisheries Research* **77**:23–247.

497 Grandcourt EM, Abdessalaam TZA, Francis, Shamsi ATA. 2005. Preliminary assessment
498 of the biology and fishery for the narrow-barred Spanish mackerel, *Scomberomorus*
499 *commerson* (Lacépède, 1800), in the southern Arabian Gulf. *Fisheries Research* **76**: 277–
500 290.

501 Hilborn R, Walters CJ. 1992. Quantitative Fisheries Stock Assessment. *Reviews in Fish*
502 *Biology and Fisheries* **2**: 177–178.

503 Juan-Jordá MJ, Mosqueira I, Cooper AB, Freire J, Dulvy NK. 2011. Global population
504 trajectories of tunas and their relatives. *Proceedings of the National Academy of Sciences of*
505 *the United States of America* **51**: 20650–20655.

506 Laliberte AS, Ripple WJ. 2004. Range Contractions of North American Carnivores and
507 Ungulates. *BioScience* **54**:123.

508 McClenachan L, Cooper AB. 2008. Extinction rate, historical population structure and
509 ecological role of the Caribbean monk seal. *Proceedings of the Royal Society B: Biological*
510 *Sciences* **275**:1351–1358.

511 McPherson GR. 1985. Development of the northern Queensland mackerel fishery.
512 *Australian Fisheries* **44**:15–17.

513 McPherson GR. 2007. Historical stock definition research on *Scomberomorus commerson* in
514 Queensland waters. Pages 33–60 in RC Buckworth, SJ Newman, JR Ovenden, RJG Lester,
515 and GR McPherson, editors. *The Stock Structure of Northern and Western Australian*
516 *Spanish Mackerel*. Northern Territory Government, Australia. Fishery Report FRDC 98/159.

517 Munro I. 1942. The eggs and early larvae of the Australian barred Spanish mackerel,
518 *Scomberomorus commersoni* (Lacépède) with preliminary notes on the spawning of that
519 species. *Proceedings of the Royal Society of Queensland* **54**:33–48.

520 National Library of Australia. 2014. Available from <http://www.trove.nla.gov.au> (accessed
521 July 2014).

522 O'Neill MF, Courtney AJ, Turnbull CT, Good NM, Yeomans KM, Smith JS, Shootingstar C.
523 2003. Comparison of relative fishing power between different sectors of the Queensland
524 trawl fishery, Australia. *Fisheries Research* **65**:309–321.

525 Russell MW, Pears R. 2008. Workshop Summary: Management and Science of Fish
526 Spawning Aggregations in the Great Barrier Reef Marine Park 12-13 July 2007. Great
527 Barrier Reef Marine Park Authority, Townsville.

528 Sadovy YJ. 2003. Fisher survey interview format general guidelines. Society for the
529 Conservation of Reef Fish Aggregations.

530 Sadovy Y, Eklund AM. 1999. Synopsis of biological data on the Nassau grouper,
531 *Epinephelus striatus* (Bloch, 1792), and the jewfish, *E. itajara* (Lichenstein, 1822).

532 NOAA/National Marine Fisheries Service.

533 Sadovy de Mitcheson YS, Cornish A, Domeier M, Colin PL, Russekk M, Lindeman, KC.
534 2008. A Global Baseline for Spawning Aggregations of Reef Fishes. *Conservation Biology*
535 **22**:1233–1244.

536 Sadovy de Mitcheson Y, Erisman BE. 2012. *Fishery and Biological Implications of Fishing*
537 *Spawning Aggregations, and the Social and Economic Importance of Aggregating Fishes.*
538 *Pages 225–284 Reef Fish Spawning Aggregations: Biology, Research and Management.*
539 Fish and Fisheries Series Volume 35.

540 Safina C. 1994. Where have all the fishes gone. *Issues in Science and Technology* **10**: 37-43.

541 Shepherd TD, Litvak ML. 2004. Density-dependent habitat selection and the ideal free
542 distribution in marine fish spatial dynamics: considerations and cautions. *Fish and Fisheries*
543 **5**: 141- 152.

544 Tobin, A., L. Currey, and C. Simpfendorfer. 2013. Informing the vulnerability of species to
545 spawning aggregation fishing using commercial catch data. *Fisheries Research* **143**:47–56.

546 Tobin A, Heupel M, Simpfendorfer C, Pandolfi JM, Thurstan RH, Buckley SM. 2014.
547 Utilising innovative technology to better understand spawning aggregations and he
548 protection offered by marine protected areas. FRDC 2010/007.

549 Townsville Daily Bulletin. 1934. Available from
550 [http://trove.nla.gov.au/ndp/del/article/61866410?searchTerm=king%20fish&searchLimits=1-](http://trove.nla.gov.au/ndp/del/article/61866410?searchTerm=king%20fish&searchLimits=1-state=Queensland%7C%7C%7Ctitle=97%7C%7C%7C-decade=193)
551 [state=Queensland%7C%7C%7Ctitle=97%7C%7C%7C-decade=193](http://trove.nla.gov.au/ndp/del/article/61866410?searchTerm=king%20fish&searchLimits=1-state=Queensland%7C%7C%7Ctitle=97%7C%7C%7C-decade=193) (accessed July 1934).

552 Webb TJ, Noble D, Freckleton RP. 2007. Abundance-occupancy dynamics in a human
553 dominated environment: linking interspecific and intraspecific trends in British farmland and
554 woodland birds. *Journal of Animal Ecology* **76**: 123-134.

555 Webb TJ, Dulvy NK, Jennings S, Polunin NV. 2011. The birds and the seas: body size
556 reconciles differences in the abundance-occupancy relationship across marine and terrestrial
557 vertebrates. *Oikos* **120**: 537–549.

558 Webb TJ, Freckleton RP, Gaston KJ. 2012. Characterizing abundance-occupancy
559 relationships: there is no artefact. *Global Ecology and Biogeography* **21**: 952–957.
560
561