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The balancing act of captive breeding programmes: salmon stocking and angler catch statistics

K. A. YOUNG

Natural Resources Wales, Cardiff, UK

Abstract The debate over Atlantic salmon, *Salmo salar* L., stocking in Britain centres on the trade-off between enhancing rod fisheries and harming wild populations. This article informs the debate by quantifying the relationship between stocking and angler catch statistics for 62 rivers over 15 years. After controlling for environmental factors affecting adult abundance, the 42 rivers with stocking had non-significantly lower mean catch statistics than the 20 rivers without stocking. This difference increased with the age of stocked fish. Among stocked rivers, weak relationships between mean stocking effort and catch statistics also became more negative with the age of stocked fish. For stocked rivers, there was no evidence for a generally positive relationship between annual stocking efforts and catch statistics. Those rivers for which stocking appeared to improve annual rod catches tended to have lower than expected mean rod catches. The results suggest the damage inflicted on wild salmon populations by stocking is not balanced by detectable benefits to rod fisheries.

KEYWORDS: angling, fisheries, hatcheries, recreational catch, *Salmo salar*, stocking enhancement.

Introduction

Captive breeding programmes can help conserve species at risk of local extirpation or extinction, but impose a range of ecological and evolutionary risks (Snyder *et al.* 1996; Blanchet *et al.* 2008; Fraser 2008; Neff *et al.* 2011). Assessing the trade-off between demographic enhancement and damage to wild populations using imperfect data is a fundamental challenge in fisheries management. The challenge is further complicated when politically empowered resource users exploit economically valuable species (Van Poorten *et al.* 2011). This scenario is epitomised by Atlantic salmon, *Salmo salar* L., management in Britain, where the value of privately owned river fisheries is determined by the number of adults returning from the marine environment. In anadromous Atlantic salmon, density-dependent population regulation occurs principally in the freshwater rather than marine environment (Milner *et al.* 2003; Friedland *et al.* 2009). Stocking captive reared juveniles is promoted by fishery owners as an effective method to increase adult abundance and enhance fisheries (Aprahamian *et al.* 2003), and political pressure from anglers results in considerable public resources being used to support captive breeding programmes.

Atlantic salmon has been stocked into European rivers since the time of Darwin, and by the middle of the 20th Century large-scale hatcheries were popular management tools for both Atlantic and Pacific salmon (*Oncorhynchus* spp.). A mature body of evidence underpins the scientific consensus that captive breeding programmes threaten wild salmon and where protecting wild stocks is a management priority, should be considered only for the demographic rescue of populations at immediate risk of extirpation (e.g. Chilcote *et al.* 1986, 2011; Hilborn 1992; Meffe 1992; Waples 1999; Levin *et al.* 2001; Levin & Williams 2002; Ruckelshaus *et al.* 2002; Chilcote 2003; Nickelson 2003; Ford *et al.* 2006; Araki *et al.* 2007b, 2008, 2009; Blanchet *et al.* 2008; Fraser 2008; Naish *et al.* 2008; Buhle *et al.* 2009; RIST 2009; Bailey *et al.* 2010; European Commission 2011; Neff *et al.* 2011; Christie *et al.* 2012; Palmé *et al.* 2012).

In England and Wales, stocking continues in viable wild populations principally due to political pressure from anglers. Managers have realised a gradual shift from traditional hatchery to wild broodstock programmes, where a small proportion of adults is captured, bred, and their offspring reared and released. The threat to wild populations is presumably reduced because relatively few juveniles are stocked, and large proportions of

Correspondence: Kyle A. Young, Natural Resources Wales, Cambria House, Newport Road, CF24 0TP Cardiff, UK (e-mail: kyle.young@naturalresourceswales.gov.uk)

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populations are not subjected to serial episodes of artificial selection in the hatchery environment (Blanchet *et al.* 2008; RIST 2009; Neff *et al.* 2011). The few detailed studies using DNA parentage analysis reveal wild broodstock schemes can yield single-generation increases in adult abundance (Araki *et al.* 2007b; Caroffino *et al.* 2008; Theriault *et al.* 2010; Christie *et al.* 2012). However, the evolutionary response to hatchery induced artificial selection can be as rapid as a single generation (Araki *et al.* 2007b; Blanchet *et al.* 2008; Christie *et al.* 2012), and result in reductions to individual fitness and wild population productivity in subsequent generations (Araki *et al.* 2007b, 2009; Williamson *et al.* 2010; Chilcote *et al.* 2011; Neff *et al.* 2011; Christie *et al.* 2012).

Resolving the disconnect between scientific consensus and management practice requires quantifying the cumulative demographic effects of contemporary stocking programmes on adult salmon abundance. For anglers, it is this cumulative demographic effect, not the size or integrity of wild populations, that motivates political pressure to continue stocking. The aim of the present article was to quantify the relationship between Atlantic salmon stocking and angler catch statistics in England and Wales. The results suggest that stocking is associated with small reductions in angler catch statistics and by inference, adult abundance.

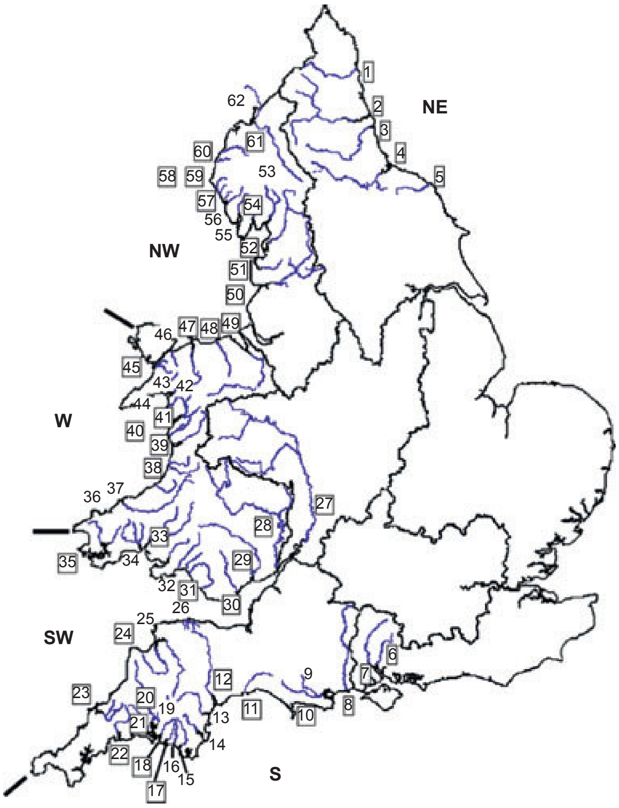

Figure 1. Map of the 62 study catchments in England and Wales. Bold lines and letters adjacent to the map indicate 'regions'. Boxed numbers are catchments with at least one stocking event during the study period. Catchment names and relevant data are presented in Table 1.

Materials and methods

The following data were collected for 62 river catchments in England and Wales (Fig. 1, Table 1; Cefas 2010): habitat area, habitat quality and Conservation Limit (CL). Habitat area (ha) is an estimate of the wetted area available to anadromous salmon. Habitat quality (number of eggs $100\ \mathrm{m}^{-2}$) is an estimate of the average carrying capacity for juvenile salmon in that area (Wyatt & Barnard 1997; Cefas 2010). The CL (no of eggs) combines habitat area and habitat quality to provide an estimate of the total number of eggs required to seed the juvenile habitat of a catchment (Cefas 2010). The CL provides a proxy for a catchment's carrying capacity and is used by the Environment Agency for stock assessments of adult escapement. Here, the CL provides an estimate of 'natural adult stock size' based on the relationship between juvenile carrying capacity, smolt production and adult population size at the catchment scale.

Annual estimates of two angler catch statistics, total rod catch (rod catch) and number of salmon caught per license day of fishing effort (CPLD), for the 62 catchments between 1995 and 2009 were taken from Environment Agency reports. Missing data resulted in 911 and 925 observations for rod catch and CPLD respectively (Fig. 2). Few stocked fish are marked and anglers are not required to record marks in their catch returns, so catch data cannot be used to estimate the relative contributions of wild and stocked fish to rod fisheries.

Stocking data were taken from Agency reports and internal records (for data from 1992 to 1994). Stocking data were compiled at the catchment scale to match the catch statistics. Catchments with stocking had greater habitat area than those without [mean (SD) of $\log_{10}$ (ha): $n = 42$, 2.1 (0.53) and $n = 20$, 1.7 (0.45), respectively, pooled variance $t_{60} = 2.7$, $P < 0.01$], but stocked and unstocked catchments had similar habitat qualities [215 (48) vs 226 (58), $t_{60} = 0.75$, $P = 0.46$].

Stocked fish were grouped into three age classes: young-of-year (YOY) fish (i.e. ova to fry), 1-year-old parr and smolts ready for migration to sea. The three age classes were assigned to a year's catch statistics by assuming all stocked fish spent two winters in fresh water and returned as adults after a single winter at sea, which is the most common life history of wild and stocked salmon in England and Wales. Thus, YOY, parr

Table 1. Catchment variables, catch statistic and stocking effort summary statistics for the 62 study rivers: Map code (see Fig. 1); River name (common local name); Area (ha of habitat available to anadromous salmon in the river catchment); Habitat quality (an estimate of the number eggs 100 m^{-2} required to seed average habitat); CL (Conservation Limit; the number of eggs × 10^6 required to seed the entire catchment with juvenile salmon); Rod catch (the mean total number of salmon reported caught between 1995 and 2009); CPLD (the mean Catch Per License Day of fishing effort between 1995 and 2009); Years (the number of years affected by stocking between 1995 and 2009); Total (mean stocking effort of all age classes × 10^3); YOY (mean Young of the Year stocking effort × 10^3); Parr (mean parr stocking effort × 10^3); Smolt (mean smolt stocking effort × 10^3)

Map code	River name	Area	Habitat quality	CL	Rod catch	CPLD	Years	Total	YOY	Parr	Smolt
1	Coquet	144	218	3.14	682	0.10	2	16.4	12.3	4.1	0.0
2	Tyne	542	208	11.25	2579	0.13	15	727.5	635.4	91.5	0.6
3	Wear	232	250	5.80	587	0.06	3	2.8	0.0	2.8	0.0
4	Tees	620	240	14.90	113	0.05	5	129.7	120.0	9.7	0.0
5	Yorkshire Esk	86	236	2.02	78	0.05	15	73.4	70.9	2.5	0.0
6	Itchen	69	234	1.63	158	0.20	11	40.0	40.0	0.0	0.0
7	Test	138	246	3.40	214	0.13	11	244.0	243.9	0.1	0.0
8	Hampshire Avon	369	175	6.48	80	0.05	5	5.9	4.4	1.5	0.0
9	Piddle	18	177	0.31	5	0.03	0	–	–	–	–
10	Frome	88	171	1.50	87	0.09	1	4.0	4.0	0.0	0.0
11	Axe	83	175	1.45	16	0.01	10	12.8	10.1	0.8	1.9
12	Exe	282	253	7.14	412	0.14	6	4.6	3.9	0.0	0.8
13	Teign	98	251	2.47	112	0.06	0	–	–	–	–
14	Dart	137	218	2.98	94	0.05	0	–	–	–	–
15	Devon Avon	35	202	0.70	38	0.04	0	–	–	–	–
16	Erme	20	180	0.37	7	0.06	0	–	–	–	–
17	Yealm	11	212	0.24	6	0.04	1	0.4	0.4	0.0	0.0
18	Plym	29	188	0.55	18	0.05	1	0.9	0.9	0.0	0.0
19	Tavy	68	201	1.37	66	0.07	0	–	–	–	–
20	Tamar	293	395	11.56	238	0.10	9	24.8	19.0	0.7	5.1
21	Lynher	29	233	0.68	54	0.07	5	9.9	9.9	0.0	0.0
22	Fowey	42	207	0.86	153	0.05	4	22.7	22.7	0.0	0.0
23	Camel	56	176	0.98	294	0.08	4	25.0	25.0	0.0	0.0
24	Torridge	198	207	4.10	63	0.04	6	6.6	6.1	0.3	0.2
25	Taw	274	211	5.78	249	0.09	0	–	–	–	–
26	Lyn	27	359	0.97	145	0.29	0	–	–	–	–
27	Severn	898	143	12.85	314	0.04	14	328.4	305.1	19.8	3.5
28	Wye	1610	221	35.66	769	0.09	4	54.6	51.0	1.7	1.8
29	Usk	407	248	10.11	727	0.13	3	4.3	4.0	0.2	0.1
30	Taff	146	219	3.19	27	0.05	15	87.9	40.8	13.6	33.5
31	Ogmore	61	180	1.10	63	0.02	4	4.7	0.0	1.8	2.9
32	Tawe	88	211	1.85	121	0.06	0	–	–	–	–
33	Tywi	500	226	11.30	499	0.03	3	17.5	12.7	4.0	0.8
34	Taf	90	189	1.70	76	0.04	0	–	–	–	–
35	Cleddau	87	179	1.55	49	0.02	2	2.7	0.0	0.9	1.8
36	Nevern	19	259	0.48	32	0.02	0	–	–	–	–
37	Teifi	326	265	8.65	556	0.04	0	–	–	–	–
38	Rheidol	31	222	0.68	35	0.02	1	0.3	0.0	0.3	0.0
39	Dyfi	179	235	4.21	138	0.06	2	3.7	1.7	2.0	0.0
40	Dysynni	31	216	0.68	4	0.00	1	1.3	1.3	0.0	0.0
41	Mawddach	57	242	1.37	125	0.03	15	54.3	46.9	3.7	3.7
42	Dwyryd	9	201	0.19	19	0.05	0	–	–	–	–
43	Glaslyn	25	191	0.48	23	0.02	0	–	–	–	–
44	Dwyfawr	33	258	0.86	14	0.01	0	–	–	–	–
45	Seiont	21	226	0.48	34	0.04	2	1.6	1.6	0.0	0.0
46	Ogwen	24	362	0.87	87	0.10	0	–	–	–	–
47	Conwy	50	127	0.63	169	0.07	14	104.5	97.3	0.3	6.9
48	Clwyd	84	237	1.99	70	0.02	14	65.1	61.0	0.5	3.6

(continued)

Table 1. (continued)

Map code	River name	Area	Habitat quality	CL	Rod catch	CPLD	Years	Total	YOY	Parr	Smolt
49	Dee	617	248	15.30	591	0.07	15	313.1	276.8	15.4	21.0
50	Ribble	351	242	8.49	805	0.08	13	104.1	96.6	5.4	2.1
51	Wyre	67	70	0.47	12	0.05	4	39.6	39.1	0.5	0.0
52	Lune	423	280	11.84	1349	0.10	14	646.4	629.1	11.8	5.5
53	Kent	68	223	1.52	449	0.11	0	–	–	–	–
54	Leven	46	182	0.83	37	0.08	4	12.5	12.5	0.0	0.0
55	Duddon	26	121	0.31	39	0.09	0	–	–	–	–
56	Cumbrian Esk	20	181	0.37	75	0.13	0	–	–	–	–
57	Irt	35	198	0.69	100	0.11	2	3.0	3.0	0.0	0.0
58	Ehen	41	230	0.94	265	0.09	1	1.7	1.7	0.0	0.0
59	Calder	13	261	0.33	44	0.16	4	26.7	25.8	0.9	0.0
60	Derwent	213	185	3.93	985	0.17	6	118.8	118.3	0.5	0.0
61	Eden	688	200	13.75	1465	0.12	10	143.8	141.2	2.6	0.0
62	Border Esk	306	255	7.79	738	0.18	0	–	–	–	–

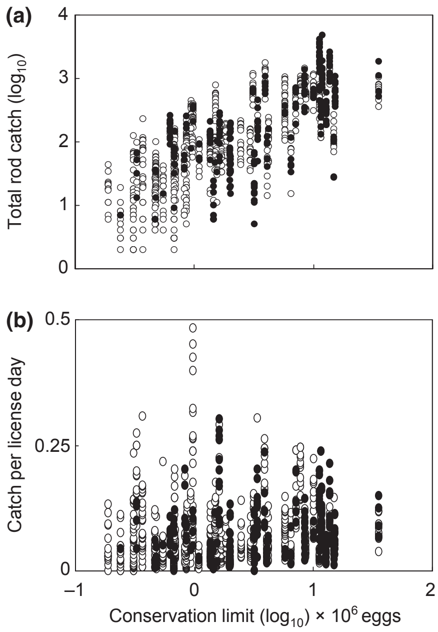

Figure 2. Observations of angler catch statistics between 1995 and 2009 from 62 rivers relative to their conservation limit (CL), an estimate of a catchment's carrying capacity as the number of eggs required to seed available habitat with juveniles. Filled symbols represent observations associated with stocking events.

and smolt stocking efforts were assigned to catch statistics 3, 2 and 1 years after stocking respectively. Total stocking efforts were dominated by YOY (Table 1), and mean absolute ($\log_{10}$) and relative [%CL = (effort/CL) × 100] stocking efforts were severely skewed for both total and age-specific components (Fig. 3). Annual efforts were similarly skewed but had higher proportions of zero values. The number of years a catchment was stocked and mean total stocking effort were strongly correlated across the 42 stocked catchments (rank correlation: absolute effort, $r_s = 0.85$, $P < 0.001$; relative effort $r_s = 0.64$, $P < 0.001$; Table 1).

Estuarine net fisheries operated on 43 of the catchments during the study period. Catchments with and without stocking were equally likely to have net fisheries (29/42 vs 14/20, $\chi^2 = 0.05$, d.f. = 1; $P = 0.83$). Net fisheries usually affect a single catchment. Where a net fishery operated in an estuary shared by two catchments, the net catch was apportioned to catchments proportional to their CLs. For the five catchments in northeast England affected principally by a near-shore net fishery (Fig. 1), total net catch was adjusted for adults leaving the study area (destined for Scottish rivers) then apportioned to the five catchments by the same method (Cefas 2010; I.C. Russell, unpublished data).

To control for the effects of net fisheries, rod catch statistics were adjusted by assuming that all fish captured would have entered rod fisheries and been exploited at the same rate as fish not captured. Estimates of rod fishery exploitation rates during the 15-year study period were taken from six rivers with fish counters (Cefas 2010). The grand mean (±95% CI) of these 90 estimates was 14.5% (±0.02%). All analyses were repeated using catch statistics adjusted upward by an amount based on 10, 15, and 20% of the net catch being captured by the rod fishery. The results were qualitatively similar to those using the unadjusted catch statistics and are not presented.

Analysis

All tests of relationships between stocking and catch statistics used river as the unit of independent observation. All analyses were repeated using absolute and relative stocking effort because the measures are not perfectly

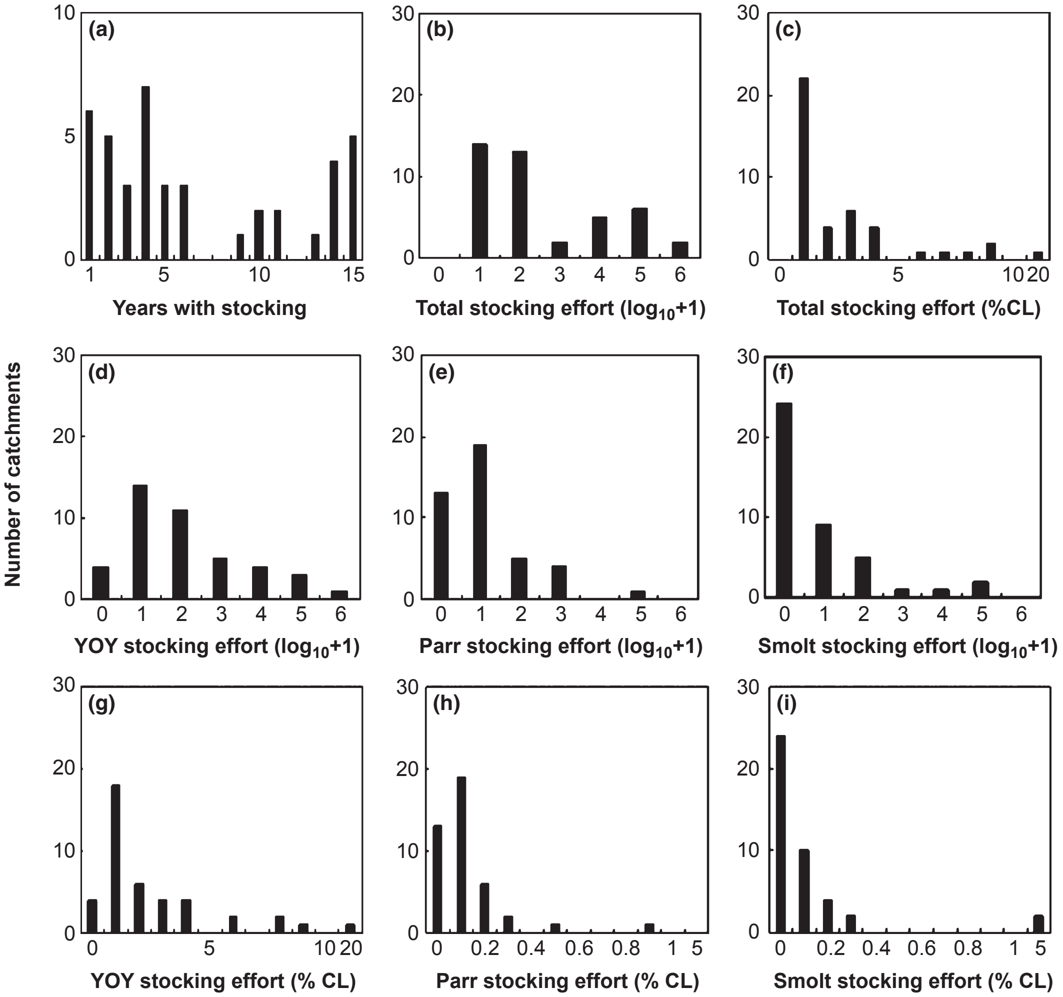

Figure 3. Distributions of number of years with stocking (a), mean absolute (b, d–f) and mean relative (c, g–i) stocking efforts for 42 stocked catchments. Young-of-the-year (YOY) effort includes egg and yearling fry; parr effort includes 1–2-year-old juveniles; smolt effort includes stocked fish ready to migrate to the marine environment. The conservation limit (CL) is an estimate of a catchment's carrying capacity as the number of eggs required to seed available habitat with juveniles.

correlated and may affect adult abundance through different ecological and evolutionary mechanisms (Nickelson 2003; RIST 2009). The results were qualitatively similar and those based on relative stocking efforts are presented.

The first analyses tested for the effects of stocking on catch statistics over the entire study period. To control for the effects of natural spatiotemporal variation in adult abundance on catch statistics, simple first order General Linear Models (Type III Sums-of-Squares) were built with two class and two continuous variables (Bolker *et al.* 2008): *Region* (Fig. 1, class), to control for variation in climate and near-shore marine conditions; *year* (class), to control for interannual variation in freshwater and marine survival; $\log_{10}$ (*area*; continuous), to control for the effects of habitat area; *habitat quality* (continuous), to control for the effects of habitat quality. The model explained 62 and 34% of the variation in rod catch and CPLD respectively. For each catchment, the means of the residuals were calculated and used as independent observations. The effects of stocking on rod catch and CPLD were tested by comparing the means of stocked and unstocked catchments (two sample *t*-tests). For stocked catchments, the relationships between mean stocking effort and mean catch statistics were tested using rank correlation.

The second analyses quantified the relationships between annual stocking efforts and annual catch statistics for the 42 stocked catchments. To control for between catchment variation in all measured (above) and unmeasured environmental factors (e.g. water quality, land use), the annual catch statistics were adjusted by subtracting the mean value from each observation for each catchment separately. These adjusted catch statistics had mean = 0 for each catchment; importantly, not dividing by the standard deviation retained catchment differences in variability around this common mean. The effect of natural inter-annual variation on the adjusted catch statistics was controlled for using a GLM with year as the single class variable. The model explained 21 and 38% of the variation in adjusted rod catch and CPLD respectively. For each catchment, the Pearson correlation coefficient between the residuals from these models and annual stocking efforts was calculated. Parametric correlation was used because it is affected by the magnitude of the observations and the individual coefficients were not used for hypothesis testing. Relationships between annual stocking efforts and annual catch statistics were tested two ways. First, binomial tests were used to determine if the signs of the correlation coefficients between indices of annual stocking effort and the residuals of annual rod catch and CPLD tended to be positive or negative. Second, the means and 95% CIs of the correlation coefficients were calculated to determine if their values were significantly different from zero.

The final analyses tested the prediction that if stocking increases catch statistics, then catchments for which annual stocking efforts are positively correlated with annual catch statistics should have higher than expected mean catch statistics, i.e. annual stocking effort vs adjusted catch statistic correlations (second analyses) should be positively related to the mean catch statistics (first analyses). This prediction was tested using Pearson correlation.

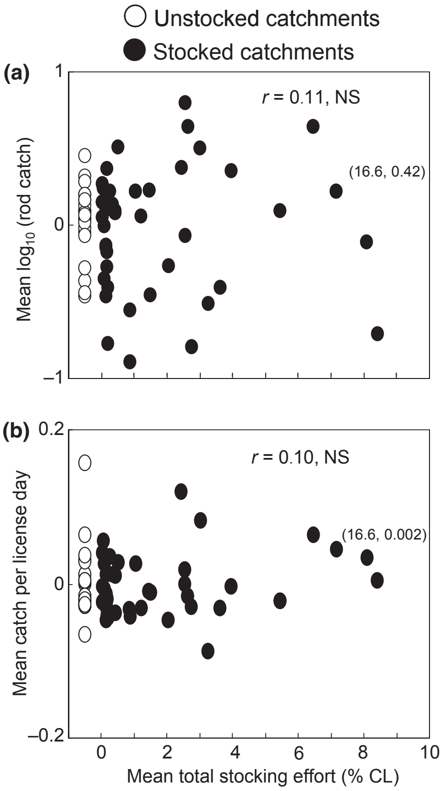

Figure 4. Catchment means of residual (a) total rod catch and (b) catch per license day for rivers with (n = 42) and without stocking (n = 20). The conservation limit (CL) is an estimate of a catchment's carrying capacity as the number of eggs required to seed available habitat with juveniles. One stocked river had a mean stocking effort beyond the range of the x-axes (16.6%). Confidence intervals for the means are not shown for clarity. The non-parametric correlation coefficients between mean stocking effort and mean residual catch statistics are shown for the 42 stocked catchments.

Results

The 42 stocked catchments had non-significantly lower mean residual catch statistics than the 20 unstocked catchments (rod catch: $t_{60} = 0.31$, $P = 0.76$; CPLD: $t_{60} = 0.53$, $P = 0.6$; Fig. 4). This difference became more pronounced with the age of stocked fish. Catchments with fry stocking ($n = 38$) had non-significantly lower rod catch ($t_{60} = 0.39$, $P = 0.69$) and higher CPLD ($t_{60} = 0.15$, $P = 0.88$). Those with parr stocking ($n = 29$) had non-significantly lower catch rod catch ($t_{60} = 1.36$, $P = 0.18$) and CPLD ($t_{60} = 1.28$, $P = 0.20$). Catchments with smolt stocking ($n = 18$) had lower rod catch ($t_{60} = 0.74$, $P = 0.46$) and significantly lower CPLD ($t_{60} = 2.03$, $P < 0.05$).

Mean catch statistics did not increase with mean total stocking effort among the 42 stocked catchments (Fig. 4). The relationship between mean stocking effort and mean catch statistics became increasingly negative with the age of stocked fish: YOY ($n = 38$, rod catch/CPLD, $r_s = 0.17/0.09$, $P > 0.20$), parr ($n = 29$, $r_s = -0.04/-0.07$, $P > 0.20$), smolts ($n = 18$, $r_s = -0.17/-0.37$, $P > 0.20$).

The correlation coefficients between total and age-specific annual stocking efforts and annual adjusted angler catch statistics for the 42 stocked catchments were evenly distributed between positive and negative (Fig. 5; binomial tests, all $P > 0.4$). In no case was the mean of the correlation coefficients significantly different from zero (all $P > 0.5$).

The annual stocking effort vs catch statistic correlations across the eight samples used in Figure 5, were not consistently related to mean stocking effort (5/8 correlations > 0; $-0.19 < r_s < 0.09$, all $P > 0.05$), variation in stocking effort (5/8 < 0; $-0.27 < r_s < 0.07$, all $P > 0.05$),

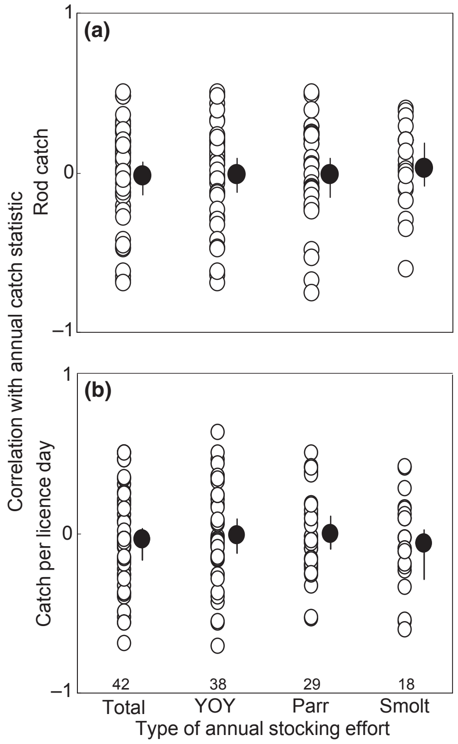

Figure 5. Pearson correlation coefficients between residual adjusted (a) rod catch and (b) catch per license day, and four indices of annual stocking effort. The numbers above the *x*-axes are the sample sizes. Solid symbols are means with 95% confidence intervals.

or variation in catch statistics ($5/8 > 0$; $-0.45 < r_s < 0.21$, all $P > 0.01$). Similarly, the absolute value of the annual effort vs catch statistic correlations did not vary systematically with variation in stocking efforts or catch statistics. The Coefficients of Variation (CV) in total stocking effort decreased with mean stocking effort ($r_s = -0.58$, $P < 0.001$) and CL ($r_s = -0.44$, $P < 0.01$), and the CVs of both catch statistics (unadjusted data) decreased with CL ($-0.29 < r_p < -0.24$, $P > 0.05$).

Negative (non-significant) relationships were found between the annual total stocking effort vs catch statistic correlations and the means of residual rod catch and CPLD (Fig. 6). For rod catch, the relationship was significantly negative when two outliers (in the bottom left of the figure) were excluded; stocking programmes that increased annual rod catch were associated with lower than expected mean rod catch. The annual total stocking effort vs rod catch correlations were also negatively related to mean escapement between 1995 and 2009 (mean = 122% of the CL, SD = 91%) including ($r_s = -0.28$, $P > 0.05$) and excluding the two outliers ($r_s = -0.45$, $P < 0.01$) of Figure 6a (data not shown).

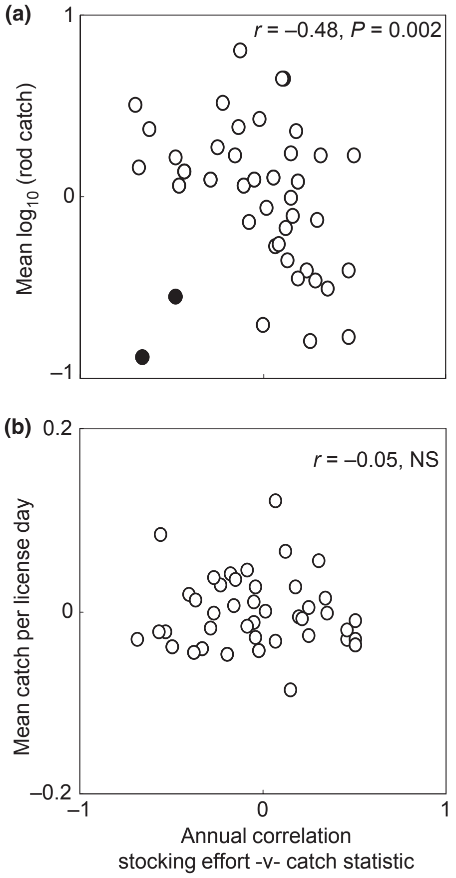

Figure 6. Relationships between the annual total stocking effort vs catch correlation coefficients and the mean residual (a) rod catch and (b) catch per license day for the 42 stocked catchments. Pearson correlation for rod catch was calculated excluding the two solid outliers in the bottom left of the panel.

Discussion

Stocking, angler catch statistics, and adult abundance

Rod catch data can meaningfully reflect variation in adult Atlantic salmon abundance (Fig. 2; Crozier & Kennedy 2001). While genetic parentage analysis can provide detailed insight into the effects of stocking in intensively studied populations (Araki *et al.* 2007a,b; Caroffino *et al.* 2008; Theriault *et al.* 2010; Christie *et al.* 2012), angler catch statistics typically provide the only data available to managers for studying broad-scale spatiotemporal variation in anadromous salmonid adult abundance (e.g. Smith *et al.* 2000).

Beyond sampling error, there are a number of reasons catch statistics may not be sensitive enough to detect the effect of stocking on adult abundance. First, stocking and catch data are typically compiled at the catchment scale, but the stocking of juveniles and catching of adults vary at the sub-catchment scale. Stocking may increase or decrease adult abundance at smaller spatial scales, but those effects may not be detectable using catchment scale data. Second, in England and Wales adults used in captive breeding programmes are typically collected after the close of the angling season. This may impose artificial selection for or against late migration depending on the relative fitness of captive bred adults and their offspring. Because adult migration timing is heritable (Garcia de Leaniz *et al.* 2007; Carlson & Seamons 2008), stocking may principally affect the abundance of late-migrating adults that are less likely to be sampled by the rod fisheries.

The structure of the data may limit their ability to reveal the effects of stocking on adult abundance. Large stocking programmes and those targeting large stocks tended to have less variable total stocking efforts, and large catchments tended to have less variable catch statistics. The latter pattern is expected because in larger stocks environmental and life history diversity among sub-populations act to dampen temporal variation in adult abundance (Einum *et al.* 2003; Schindler *et al.* 2010). The patterns of variation in stocking effort and catch statistics combined with large stocking programmes targeting large stocks likely make it difficult to detect the potential demographic effect of stocking.

Ecological and evolutionary mechanisms

To the degree rod catch data reflect adult abundance and unmeasured environmental variables that affect adult abundance vary randomly relative to the hypotheses tested, the results suggest: stocked catchments have lower than expected mean adult abundance, mean adult abundance declines with mean stocking effort, that both patterns become more pronounced with the age of stocked fish, and that these cumulative demographic effects are small. These observations were consistent with previous research on the evolutionary ecology of salmon stocking.

The lifetime fitness (number of returning adults produced) of captive-bred wild adults is typically higher than that of wild adults that spawn the wild (Araki *et al.* 2007a; Caroffino *et al.* 2008; Theriault *et al.* 2010; Christie *et al.* 2012). However, the effect on adult abundance in the next generation may be small, even for sizable stocking programmes. For example, the River Spey Fishery Board in Scotland spends over £100 000 annually to rear and release approximately 1 million Atlantic salmon fry (Association of Salmon Fishery Boards 2011). Recent genetic parentage analysis revealed that 0.5% (3 in 558) of rod caught fish were of hatchery origin, meaning that in 2009 stocking increased total rod catch (8626) by ≈45 fish. The River Spey study suggests the YOY stocking effort to rod catch ratio required to increase rod catch by 1% is ≈230 (2 million YOY per 8671 rod caught fish). By comparison, the median/mean values of this ratio for the 42 stocked catchments were, by type of stocking effort: total = 113/430, YOY = 134/404, parr = 10/36, smolt = 16/92 (age specific ratios calculated using only catchments with age specific efforts, Table 1). Although the proportion of stocked fish surviving to smoltification should increase with the age of stocked fish (Aprahamian *et al.* 2003), the scale of programmes in England and Wales suggests any single generation positive effect of stocking on subsequent adult abundance is expected to be small.

Single generation demographic gains from stocking are likely to be proportionally negated by declines in natural population productivity. Hatchery-born offspring of wild broodstock that survive to spawn have lower fitness than wild born fish (Araki *et al.* 2007b, 2009; Williamson *et al.* 2010; Christie *et al.* 2012). The evolutionary legacy of artificial selection can manifest after a single generation of captive rearing (Blanchet *et al.* 2008; Christie *et al.* 2012), persist in subsequent generations (Araki *et al.* 2009), and is expected to increase with the time hatchery-reared juveniles are exposed to artificial selection (RIST 2009; Neff *et al.* 2011). Comparative studies have demonstrated these effects scale up to affect population-level indices negatively. Chilcote (2003) and Nickelson (2003) found population productivity declined with the scale of stocking programmes in steelhead trout, *Oncorhyncus mykiss* (Walbaum), and coho salmon, *Oncorhynchus kisutch* (Walbaum) respectively. For steelhead, the Pacific species with a life history most similar to Atlantic salmon, a population with 50% hatchery origin adults would produce fewer than half the recruits per adult as a pure wild population (Chilcote 2003). Chilcote *et al.* (2011) generalised these results across species and geographic regions. Importantly, they found wild broodstock programmes were as damaging as traditional hatchery programmes to wild population productivity.

There was no evidence for a consistently positive relationship between annual stocking effort and adult abundance across stocked catchments. This may be due in part to temporal noise resulting from the assumption of an invariant life history among stocked fish. However, the annual correlations did not become more positive with the age of stocked fish (Fig. 5), as would be expected by this mechanism since the scope for expression of life history variation should decline with the age at which fish are stocked. Patterns of variation in stocking and catch data did not consistently explain variation in the signs or magnitudes of the correlation coefficients, suggesting the absence of evidence for positive demographic effects of stocking was not simply due to the structure of data.

The negative relationship between annual total stocking effort vs rod catch correlations and mean rod catch (Fig. 6a) may result from at least two non-exclusive mechanisms. Evidence supports the explanation that stocking programmes that successfully recruit adults to wild populations will proportionately reduce natural productivity and mean adult abundance (Chilcote 2003; Nickelson 2003; Araki *et al.* 2007b; Williamson *et al.* 2010; Chilcote *et al.* 2011; Christie *et al.* 2012). This explanation invokes the inherent trade off of stocking programmes: the more they increase adult abundance, the more they damage wild populations. The alternative explanation that stocking programmes are more likely to successfully recruit adults to populations that are below juvenile carrying capacity is supported by the escapement data; the values of the annual correlations decreased with mean escapement (as % of CL). Assessing the relative contributions of these two mechanisms to the pattern observed is difficult because the CL compliance and residual rod catch data are derived from the same raw catch data.

Management implications

The now mature body of evidence demonstrating that stocking harms wild salmon populations has failed to influence those promoting stocking as a responsible rod fishery enhancement tool. The challenge of translating science to management may be best met using the data most relevant to politically empowered resource users. Evidence that stocking appears to have, if anything, a small negative effect on catch statistics should resonate with anglers, and has important implications for salmon management.

In England and Wales, the Environment Agency and Natural Resources Wales are responsible for protecting wild Atlantic salmon stocks and rely on angler catch statistics for stock assessment. If stocking materially increased angler catch statistics, then managers would be unable to assess the demographic status of wild salmon populations without implementing extensive marking/reporting programmes. Detectable positive demographic effects would also increase the risk to wild populations. Alternatively, to the degree stocking has a negative effect on adult abundance, the fisheries management agencies are permitting and supporting an activity that demonstrably harms the wild salmon populations they are charged with protecting. Depending on the suite of mechanisms responsible for the present results, it may be that the political pressure to stock is being managed in a manner that limits damage to wild populations (Van Poorten *et al.* 2011). If stocking has a negligible effect on catch statistics and adult abundance principally because stocked fish do not survive to adulthood, then the results are encouraging. To the degree that stocked fish are compensating for stocking-induced reductions in wild population productivity, the results are troubling.

In the context of the broader evidence base, the present results support and extend previous management recommendations. Firstly, the debate on stocking should begin with the presumption that stocking poses a scale-dependent threat to wild populations. Where the status of wild populations is a management priority, captive breeding programmes should only be considered for populations that are at imminent risk of extirpation (Lande 1988) and protected by no-harvest regulations. Secondly, there is an urgent need to review legally mandated stocking programmes (e.g. mitigation stocking for habitat loss from drinking water reservoirs) in the context of current evidence, the scientific consensus, and contemporary legislation prioritising the protection of wild salmonids. Thirdly, fisheries managers must promote and support alternative activities (e.g. habitat restoration, juvenile fish surveys) that provide anglers the opportunity to contribute to salmon conservation efforts. Finally, analyses like those presented here should be repeated elsewhere to build an accessible evidence base that resonates with politically empowered resource users. Doing so will allow anglers to inform their opinions with materially relevant data, advance the debate on stocking, and improve the ability of managers to protect wild anadromous salmonids.

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