REVIEWS IN Aquaculture

Reviews in Aquaculture, 1–23 doi: 10.1111/raq.12277

Impacts of marine and freshwater aquaculture on wildlife: a global meta-analysis

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Received 15 January 2018; accepted 18 July 2018.

Abstract

The global expansion of aquaculture has raised concerns about its environmental impacts, including effects on wildlife. Aquaculture farms are thought to repel some species and function as either attractive population sinks ('ecological traps') or population sources for others. We conducted a systematic review and meta-analysis of empirical studies documenting interactions between aquaculture operations and vertebrate wildlife. Farms were associated with elevated local abundance and diversity of wildlife, although this overall effect was strongly driven by aggregations of wild fish at sea cages and shellfish farms (abundance: 72×; species richness: 2.0×). Birds were also more diverse at farms (1.1×), but other taxa showed variable and comparatively small effects. Larger effects were reported when researchers selected featureless or unstructured habitats as reference sites. Evidence for aggregation 'hotspots' is clear in some systems, but we cannot determine whether farms act as ecological traps for most taxa, as few studies assess either habitat preference or fitness in wildlife. Fish collected near farms were larger and heavier with no change in body condition, but also faced higher risk of disease and parasitism. Birds and mammals were frequently reported preying on stock, but little data exist on the outcomes of such interactions for birds and mammals – farms are likely to function as ecological traps for many species. We recommend researchers measure survival and reproduction in farm-associated wildlife to make direct, causal links between aquaculture and its effects on wildlife populations.

Key words: attraction, ecological traps, environmental impact, fitness, predation, wild population.

Introduction

Aquaculture infrastructure (farms hereafter) presents a novel environment for wild animal populations. High stocking densities within farms aggregate biomass far beyond natural levels (commonly 5–45 kg m^{-3} final biomass: FAO Fisheries and Aquaculture 2018) and, in open systems, provide considerable trophic subsidies for animals that take advantage of the opportunity, potentially benefitting some wildlife. However, there are also deleterious effects associated with proximity to farms, and the net impact of aquaculture on productivity and persistence of wildlife populations will depend both on behavioural responses to farms and on the fitness consequences of those responses. Where individuals are attracted to a habitat that confers poorer fitness outcomes than other available habitats, they have fallen into an 'ecological trap' (Robertson & Hutto 2006; Hale & Swearer 2016). While the concept is defined at the individual level, trap habitats have population-level consequences by drawing individuals from surrounding habitats into attractive population sinks (Hale *et al.* 2015). Even in the absence of an ecological trap, changes in the abundance and spatial distribution of influential species may indirectly affect other species and drive large-scale shifts in biodiversity and ecosystem function (Gamfeldt *et al.* 2015).

A range of attractive and repulsive mechanisms for wildlife can occur simultaneously at farms (Callier *et al.* 2017). The primary attractive mechanism in most systems is probably food availability, either in the form of direct predation on stock, or an indirect trophic subsidy in the form of farm waste (spilled feed, faeces and dead stock). Birds, pinnipeds and otters are well-documented predators of stock at sea cage or pond fish farming systems (Carss 1993; Pitt & Conover 1996; Adámek *et al.* 2003; Güçlüsoy & Savas 2003; Quick *et al.* 2004; Freitas *et al.* 2007; Dorr *et al.* 2012; Sepúlveda *et al.* 2015), while farm waste from sea cages also attracts significant aggregations of opportunistic wild fish (Dempster *et al.* 2002, 2009; Tuya *et al.* 2006; Sanchez-Jerez *et al.* 2011). A high local abundance of fish is likely to lead to secondary attraction of large predators, such as dolphins (Diaz López 2006; Piroddi *et al.* 2011). Shellfish and algae farming do not require inputs of feed, but high densities of filter feeding shellfish in farms do accumulate biomass, attracting wild fish and invertebrate species (Dealteris *et al.* 2004; Powers *et al.* 2007; McKindsey *et al.* 2011; Segvic-Bubic *et al.* 2011), while algae farming attracts wild herbivores (Hehre & Meeuwig 2016). Farm structures themselves may also be attractive, functioning in a similar manner to fish aggregation devices or artificial reefs (Tallman & Forrester 2007; Sanchez-Jerez *et al.* 2011). Farm structures provide three-dimensional habitat complexity, and associated light, noise and novel biofouling communities may all be attractive to a range of wild taxa (Dumont *et al.* 2011; Callier *et al.* 2017). Paradoxically, many of these environmental changes associated with farms, such as light, noise, eutrophication and high densities of predators, may have repulsive effects on wary or functionally specialised taxa (Markowitz *et al.* 2004; Becker *et al.* 2011).

Attraction to farms may increase or decrease the fitness of wildlife. One expectation is that increased food availability will lead to faster growth, higher body condition and increased reproductive output. Accordingly, there is some evidence that farm-associated wild fish have higher body condition and reproductive investment indices than fish from reference sites (Dempster *et al.* 2011), but little is known about potential benefits for other taxa. In broadcast spawning taxa, high local population densities at farms are likely to confer greater mating efficiency (Inglis & Gust 2003). Such benefits for farm-associated wildlife are likely to be at least partially counteracted by potential deleterious fitness effects related to dietary shifts, contamination, disease, parasitism and elevated mortality rates. For example, a shift from fish oils to terrestrially derived ingredients in aquaculture feed may result in deficiencies of long-chain polyunsaturated fatty acids in animals that feed regularly at farms (e.g. Salze *et al.* 2005; Fernandez-Jover *et al.* 2007a; Gonzalez-Silvera *et al.* 2017). Additionally, farm waste can create an anoxic environment with significant effects on benthic and estuarine communities (Wu 1995; Yucel-Gier *et al.* 2007; Herbeck *et al.* 2013; Valdemarsen *et al.* 2015), while in some areas, wildlife may also accumulate elevated tissue loadings of contaminants such as antibiotics, pyrethroid parasiticides, metals and organohalogens (Samuelsen *et al.* 1992; Boyd & Massaut 1999; Burridge *et al.* 2010; Bustnes *et al.* 2010) with potentially nontrivial effects (e.g. Crump & Trudeau 2009; Berg *et al.* 2016). For fish, the primary concern may be the effect of proximity to farms on disease and parasitism rates: high population densities within farms create favourable conditions for outbreaks of diseases and parasites such as sea lice (Krkosek *et al.* 2005, 2006; Costello 2009; Lafferty *et al.* 2015; Krkošek 2017). Wild fish populations may also act as reservoirs for parasites and diseases, and as they move between cages to take advantage of feeding opportunities, they act as potential transmission vectors that may increase reinfection rates for farms, driving positive feedbacks (Uglem *et al.* 2009; Hayward *et al.* 2011).

Despite this suite of environmental concerns, the aquaculture industry is the world's fastest-growing food production sector (FAO Fisheries and Aquaculture 2016). For this growth to be sustainable in terms of environmental impacts and 'social licence' to operate, the industry must grapple with issues arising from interactions between aquaculture activities and the natural environment and develop solutions to minimise negative effects on wildlife (and vice versa). The first step should be to assess the state of knowledge on these issues and identify the most severe effects. Recent reviews have outlined the range of interactions that occur between aquaculture activities and wild fauna (e.g. Uglem *et al.* 2014; Taranger *et al.* 2015; Callier *et al.* 2017; Glover *et al.* 2017), but there has been not yet been a quantitative global synthesis of the impacts of aquaculture on wildlife. Here, we conduct a systematic review and meta-analysis of studies documenting interactions between aquaculture activities and wildlife, primarily to quantify the effects of these interactions on abundance, diversity and fitness of farm-associated wildlife, and secondarily to highlight potential drivers of conflict between wildlife and aquaculture. Thereafter, we recommend directions for future research to address key knowledge gaps in this area.

Materials and methods

Literature search and systematic review

Primary publications up to November 2017 were discovered by searching for the following terms using the ISI Web of Science: (aquaculture OR mariculture OR 'fish farm*' OR 'shellfish farm*' OR 'mussel farm*' OR 'oyster farm*' OR 'sea cage*' OR 'net pen*' OR 'fish pond*' OR 'seaweed farm*' OR 'macroalgal farm*' OR 'algal farm*') AND (attract* OR avoid* OR wild OR aggreg* OR impact* OR depredat* OR predat* OR disease) AND (wildlife OR animal* OR fauna* OR fish* OR shark* OR mammal* OR dolphin* OR cetacean* OR otter* OR seal* OR sea lion* OR bird* OR avian OR reptile* OR snake* OR amphibian* OR frog*). >9000 results were manually screened on an individual basis, by title and abstract alone where the topic was clearly irrelevant, or else after accessing the full text. Additional articles missed by our initial search were discovered using informal exploratory searches using Google Scholar and by reading the reference lists of all relevant articles returned by our initial search. Our search focused on interactions with vertebrate wildlife (defined here as fish, birds, mammals and reptiles), as these animals are typically highly mobile and are therefore more able to make decisions about whether to reside at and interact with farms.

For inclusion, publications were required to have provided empirical field data on at least one of the following: (i) distribution, behaviour, condition, disease or mortality of wildlife in the vicinity of aquaculture sites, or (ii) direct interactions between wildlife and stock at aquaculture sites (e.g. predation of stock). To minimise potential duplication of data, we only included peer-reviewed English-language journal articles.

To document the distribution of research effort in the field, we recorded the year, country, region, environment, culture system, culture taxa and the wild taxa for each study.

Meta-analysis

Studies were included in the subsequent meta-analysis if they provided quantitative data sufficient to calculate effect sizes for variables at aquaculture sites relative to 'natural' or 'reference' sites. We extracted a range of quantitative variables that were representative of the dominant types of interactions between aquaculture operations and wild vertebrates, relating to spatial distribution (Abundance, Species Richness), size structure (Length, Weight), food availability (Body Condition, Stomach Fullness), disease and parasite infection levels – either infection loads on individuals or prevalence of infected individuals in the population (Infection Level), as well as direct measures of Mortality and Fertility. Reproductive condition metrics (e.g. relative gonad size) were considered a component of Body Condition.

Natural log response ratios were calculated for each variable: RR = $\ln(F/R)$, where F is the trait mean at farm sites and R is the trait mean at reference sites. Taking the natural log of the response ratio normalises the error distribution by reducing the influence of positive responses (Hedges *et al.* 1999). Studies employed a variety of sampling designs, including random or matched farm and reference sites, and stocked or unstocked farms. All were treated as random for the purposes of this meta-analysis, with RR calculated from the mean trait values across all farm and reference sites regardless of how sites were selected by the authors. Where multiple complementary measures were available for a response variable, we took the mean of those measures (e.g. Fulton's K, hepatosomatic index and gonadosomatic index all contribute to the Body Condition variable). Where a study provided data on a response variable from multiple species or sites, we combined data to provide a single replicate, except where data spanned multiple culture systems (e.g. cages and ponds), taxonomic classes (e.g. birds and mammals), environments (e.g. marine and freshwater) or countries. No article contributed more than two studies to our database. This was done to prevent studies that provided data on numerous species from having a disproportionate influence on our findings and to ensure spatial independence between replicates given the high mobility of most species studied. Where data were provided for farms with and without exclusion measures (e.g. fenced and unfenced sites), we used data from sites without exclusion measures.

Some variables were not easily quantified for statistical analysis but were nonetheless important in understanding interactions between farms and wild fauna. These included changes in tissue fatty acid profiles, trace elements and stable isotopes, contamination from antibiotics, heavy metals and other substances, and behavioural data such as residence time or visitation rates. For these variables, we recorded the response ratio if possible, otherwise we noted the direction or nature of the effect.

Statistical analyses

To test for a significant effect of farm association on response variables, we checked normality before conducting one sample t-tests on RR data (mean RR under null hypothesis of no farm effect = 0) using R software (R Core Team 2017).

Exploratory model selection was used to determine which of the following factors best predicted effects of farms on wildlife (abundance and species richness responses only, as remaining responses had insufficient sample sizes for exploratory analysis): Year, Country, Continent, Environment (*Marine, Freshwater*), Culture System (*Cage, Pond, Longline, Rack, Bed*), Cultured Taxa (*Fish, Shellfish, Crustacean, Alga*), Wild Taxa (*Fish, Bird, Mammal, Reptile, Amphibian*) and Reference Habitat (*Structured, Unstructured*). We fitted a global general linear model using R and employed the dredge() function in the MuMIn package (Barton 2016) to compare the second-order Akaike's information criterion (AIC_C) score of every possible subset of the global model. AIC_C includes a correction for finite sample sizes and yields more conservative models than AIC (Burnham & Anderson 2002). We selected the model with the lowest AIC_C score and then used the likelihood ratio to test whether the selected model offered a significantly better fit than the null (intercept only) model, tested the significance of model terms and then conducted post hoc tests with a Tukey correction to test pairwise effects within significant model terms.

There was orders-of-magnitude variation in RRs for abundance and species richness among studies and systems, and accordingly, the overall trends that we report may be strongly influenced by a small number of studies with unusually large RRs. To test this possibility, we conducted a sensitivity analysis by ranking studies (replicates) according to the absolute value of the RR, removing the studies with the largest RR in a stepwise fashion and rerunning the model between each removal (Bancroft *et al.* 2007; Kroeker *et al.* 2010). We then report the number of studies that can be removed from the dataset without altering the statistical significance of the farm effect.

To test whether the geographical distribution of research effort on this topic corresponds to the distribution of aquaculture production, we fitted a zero-inflated Poisson model (using the pscl package for R: Zeileis *et al.* 2008) to compare the number of studies contributed by each country with the reported aquaculture production (t) by that country (FAO Fisheries and Aquaculture 2017). To account for the large disparity in peer-reviewed English-language research output between developed and developing nations, we also included the United Nations Human Development Index as a model term (United Nations Development Programme 2017).

Results

Our searches discovered 204 relevant studies across 191 articles published between 1978 and 2017 (Appendix I). Ninety-one studies provided comparative data on wildlife populations at farms and reference sites suitable for inclusion in the meta-analysis of log response ratios (RR).

Distribution of research effort

There was a clear geographical bias in research effort within our database, with 114 peer-reviewed English-language studies conducted in Europe and 46 in North America (Fig. 1). Among nations, Norway, the United States and Spain accounted for the most research (Fig. 1). Research effort across nations was significantly predicted by an interaction between the size of the nation's aquaculture industry and the developmental index of the nation ($P = 0.03$, Table S1), wherein highly developed nations (especially those in Europe and North America: Fig. 2) with large production contributed more studies than those with low production ($P < 0.0001$, Table S1). Several major aquaculture-producing nations were either poorly represented or entirely absent from our database: most notably, mainland China is by an order of magnitude the largest aquaculture producer in the world (FAO Fisheries and Aquaculture 2017), yet was entirely absent from our database. Other leading producers, namely Indonesia, India, Vietnam, Philippines and Bangladesh, were also either absent or represented by only a single study.

Most studies in our database assessed interactions with wildlife in marine or estuarine environments (Fig. 1), despite global animal aquaculture production being considerably higher in freshwater environments (47 cf. 27 million t in 2014) (FAO Fisheries and Aquaculture 2016). A total of 105 of 144 studies in the marine environment took place at sea cage farms, while 49 of 60 freshwater systems were pond-based (Fig. 1). Fish were the most common cultured taxa studied (163 studies) – primarily salmonids

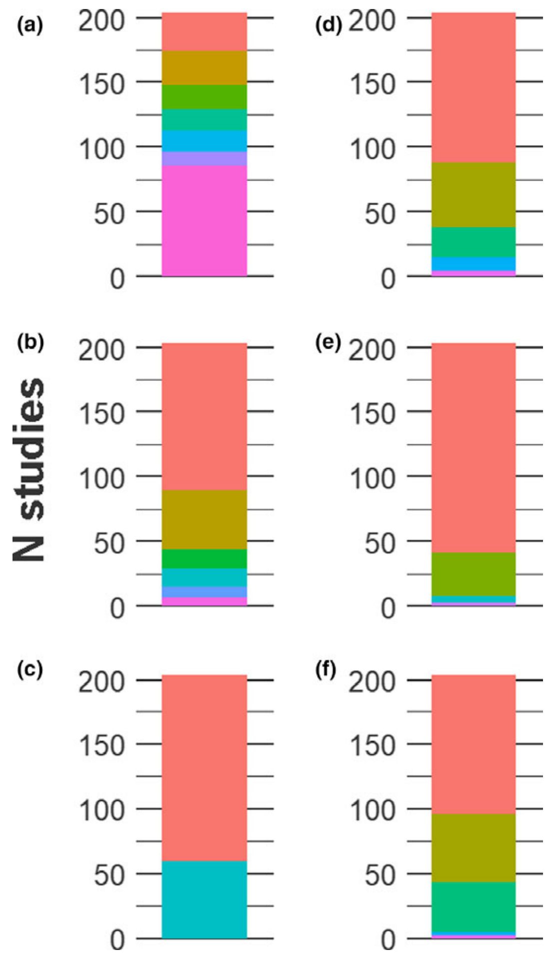

Figure 1 Distribution of research effort in terms of the number of studies that met the criteria for inclusion in our database, according to (a) Country (■) USA; (■) Spain; (■) Norway; (■) UK; (■) Canada; (■) Australia and (■) Other, (b) Culture System (■) Europe; (■) N America; (■) S America; (■) Oceania; (■) Africa and (■) Asia, (c) Region (■) Marine and (■) Freshwater, (d) Culture Taxa (■) Cage; (■) Pond; (■) Longline; (■) Rack and (■) Bed, (e) Environment (■) Fish; (■) Shellfish; (■) Alga and (■) Crustacean and (f) Wild Taxa (■) Fish; (■) Bird; (■) Mammal; (■) Reptile and (■) Amphibian.

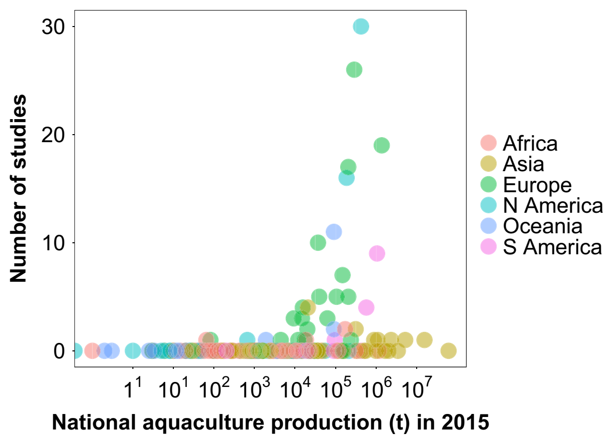

Figure 2 Distribution of research effort on interactions between aquaculture sites and wild fauna among countries and territories. Production data taken from the Fishstatj database (FAO Fisheries and Aquaculture Department 2017). (●) Africa; (●) Asia; (●) Europe; (●) N America; (●) Oceania and (●) S America.

(69 studies) in western Europe and the Americas, and sea bream (*Sparus aurata*) and sea bass (*Dicentrarchus labrax*) in southern Europe (43 studies). The research effort on environmental effects of salmon farming is in line with the predominance of salmonids in the marine fish farming sector, although freshwater cyprinid culture is the most productive pisciculture sector overall (FAO Fisheries and Aquaculture 2016). Sea bream, sea bass and marine shellfish systems are overrepresented in our dataset relative to the size of these sectors, perhaps due to their importance for nations with high marine research activity (particularly Spain). Algal and crustacean cultures (five and three studies, respectively) were dramatically underrepresented here relative to the size of the sectors (FAO Fisheries and Aquaculture 2016).

Most studies reported interactions with wild fish (108 studies), followed by birds (53 studies), mammals (38 studies), reptiles (three studies) and amphibians (two studies) (Fig. 1).

Effects on wildlife

Abundance

We discovered 65 studies that quantified the abundance of wildlife at aquaculture farming sites compared to reference sites, using various forms of control–impact (CI), before–after (BA) and control–impact-before–after (BACI) designs. These studies used a variety of sampling methods, including visual census, catch-per-unit-effort and tagging/tracking. Seventeen studies reported a lower abundance near farms, two no difference, and 46 a higher abundance. The mean effect was a 49× increase in abundance near farms (RR = 1.05, $t_{64} = 4.3$, $P < 0.0001$), but this value was strongly influenced by a few outlier studies reporting very large aggregations of wild fish around sea cages (e.g. a mean 1327× increase over three sampling dates at one Australian offshore farm compared to featureless mid-water reference sites: Dempster *et al.* 2004). Fish demonstrated the largest abundance changes, while changes in bird and mammal abundance were highly variable in both effect size and direction and not significantly different to zero (Fig. 3, Table 1). We were not able to calculate RR for an additional six studies reporting differential abundance at farms (fish: 2/2 higher; mammals: 1/2 higher; birds: 2/2 higher).

A sensitivity analysis revealed that it was possible to conduct stepwise removal of 25/65 replicates with the largest effect sizes without losing statistical significance, indicating that the overall trend was robust. However, when studies that assessed changes in wild fish abundance at sea cage systems were omitted from the analysis, the remaining studies did not provide support for an overall effect of aquaculture on wildlife abundance ($t_{38} = 0.81$, $P = 0.42$), indicating that wild fish aggregations around sea cages were largely responsible for this overall effect.

Model selection indicated that differential abundance was best predicted by a model containing Environment, Cultured Taxa and Reference Habitat ($R^2 = 0.33$, $F = 7.4$, $P < 0.0001$; Table S2). The Cultured Taxa term was significant ($P = 0.0001$), as was Reference Habitat ($P = 0.003$), while Environment was not ($P = 0.12$). Post hoc testing revealed that increases in abundance of wild fauna tended to be higher at fish farms than at shellfish farms ($P = 0.001$) and that studies comparing abundance at farm sites to unstructured or featureless reference sites (e.g.

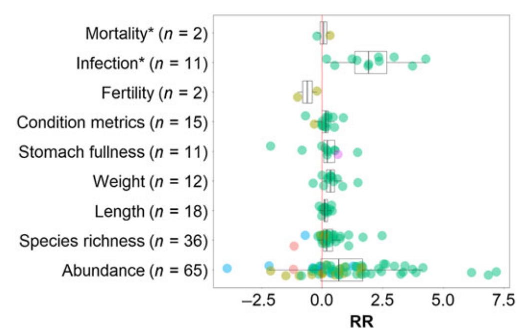

Figure 3 Summary statistics for log response ratios (RR) for each variable in our meta-analysis. All taxa are included. Boxes denote median, lower (25%) and upper (75%) quartiles, whiskers denote 1.5× interquartile range. Data points are 'jittered' for clarity. Asterisk indicates variables for which higher RR corresponds to poorer outcomes. (●) Amphibian; (●) Bird; (●) Fish; (●) Mammal and (●) Reptile.

Table 1 Mean effects of aquaculture sites on wildlife populations

	N	F:W	RR ± SE	*t*-stat	*P*
Abundance					
Fish	44	72	1.65 ± 0.29	5.7	**<0.0001**
Birds	13	1.8	0.13 ± 0.31	0.40	0.70
Mammals	7	1.1	−0.68 ± 0.67	−1.0	0.35
Amphibians	1	0.31	−1.17	–	–
All taxa	65	49	1.05 ± 0.24	4.3	**<0.0001**
Species richness					
Fish	28	2.0	0.43 ± 0.11	3.9	**0.0005**
Birds	7	1.1	0.13 ± 0.04	3.3	**0.02**
Mammals	1	0.50	−0.69	–	–
Amphibians	1	0.32	−1.15	–	–
All taxa	37	1.7	0.30 ± 0.10	3.1	**0.004**
Size (length)					
Fish	18	1.2	0.15 ± 0.03	4.6	**0.0002**
Size (weight)					
Fish	12	1.7	0.40 ± 0.13	3.0	**0.01**
Condition metrics					
Fish	14	1.3	0.17 ± 0.09	1.9	0.08
Birds	1	0.7	−0.31	–	–
All taxa	15	1.2	0.14 ± 0.09	1.5	0.15
Stomach fullness					
Fish	10	1.4	0.04 ± 0.30	0.13	0.90
Reptiles	1	1.9	0.66	–	–
All taxa	11	1.5	0.10 ± 0.28	0.35	0.73
*Infection level**					
Fish	11	16	2.09 ± 0.38	5.5	**0.0003**
Fertility					
Birds	2	0.60	−0.60 ± 0.40	−1.5	0.37
*Mortality**					
Fish	1	0.82	−0.20	–	–
Bird	1	1.4	0.33	–	–

F:W = mean at farms/mean at reference sites. RR = ln(F:W). Positive RR indicates metric is higher at aquaculture sites. *t*-stat and *P* refer to one sample *t*-test comparing RR data to null expectation of RR = 0. Taxa are omitted where no comparative data are available. Asterisk indicates variables for which higher RR corresponds to poorer outcomes. Values in bold are significant at $\alpha = 0.05$.

sandy seabed or open ocean) generally found a larger response than those that chose natural reef, unstocked farms or other structured habitats as reference sites ($P = 0.006$; Table S3).

Species richness

Most studies only assessed a limited number of target species, but 37 studies provided useful data on species richness at farms and reference sites. Of these, all but six reported higher species richness at farm sites, with a mean 1.7× increase (RR = 0.30, $t_{36} = 3.1$, $P = 0.004$). This effect was strongest in fish (RR = 0.43) but was also significant in birds (RR = 0.13) (Table 1). Only one study in our database quantified differential species richness in mammals and one in amphibians (Roycroft *et al.* 2004; Kloskowski 2010; Table 1).

There was large variation in effect size and direction across studies, but a sensitivity analysis found the overall trend to be remarkably robust (25/37 studies removed without losing statistical significance). As with abundance, the effect was not significant when sea cage systems were omitted from the analysis ($t_{21} = 1.6$, $P = 0.11$).

Species richness effects were best predicted by a model containing Reference Habitat and Wild Taxa ($R^2 = 0.27$, $F = 4.3$, $P = 0.007$; Table S2). Post hoc testing revealed that the only significant pairwise effect was between fish and amphibians, with fish species richness positively affected and amphibian species richness negatively affected by the presence of aquaculture sites in their respective environments ($P = 0.03$; Table S4).

Size structure, body condition and stomach fullness

Wild fish collected near aquaculture sites were on average 1.2× larger and 1.7× heavier than their counterparts from reference sites (Table 1), but no size comparisons were available for non-fish taxa.

Most studies (11) reported trends towards higher condition metrics in farm-associated wildlife, while two found no difference and two lower condition metrics at farms, although there was no significant effect overall (Table 1). Similarly, 8 of 11 studies found higher rates of stomach fullness in farm-associated wildlife, but these effects tended to be small and were not significant overall (Table 1). All but two comparisons of body condition or stomach fullness data concerned wild marine fish, while Gregory and Nelson (1991) estimated a 1.9× higher rate of stomach fullness in snakes at fish hatcheries, and Kloskowski *et al.* (2017) reported higher physiological stress indicators (=lower condition for our purposes) in grebes nesting on fish ponds.

Physiological changes

All 16 of 17 studies that reported looking for physiological or dietary changes in farm-associated wild fish relative to those from reference sites found evidence of dietary shifts, while the remainder found only minor differences in stable isotopes (Johnston *et al.* 2010). Evidence for dietary shift included farm feed pellets in the stomachs of farm-associated wild fish (Skog *et al.* 2003; Arechavala-Lopez *et al.* 2011; Fernandez-Jover *et al.* 2011), taxonomic changes in stomach contents (Demétrio *et al.* 2012; Fernandez-Jover & Sanchez-Jerez 2015), higher tissue fat content and altered tissue fatty acid profiles that reflected the terrestrial origin of lipids in farm feed (Skog *et al.* 2003; Fernandez-Jover *et al.* 2007a,b, 2011; Arechavala-Lopez *et al.* 2011, 2015a,b; Abaad *et al.* 2016). Arechavala-Lopez *et al.* (2015a,b) also reported differing trace element profiles in saithe near and far from salmon farms, while two studies reported altered taste and other metrics of quality (Skog *et al.* 2003; Bogdanović *et al.* 2012).

Contamination

Comparisons of contaminant levels in the tissues of farm-associated and non-associated fish revealed mixed results. All three studies that tested for antimicrobial contamination in farm-associated wild fish at farms where antimicrobials were in use found evidence of antimicrobial residue in the majority of fish sampled, including oxytetracycline (0.2–1.3 $\mu g\ g^{-1}$ muscle tissue: Björklund *et al.* 1990), oxolinic acid (0.4–4.4 $\mu g\ g^{-1}$ muscle tissue at two farms: Samuelsen *et al.* 1992) and flumequine (1.0–4.9 $\mu g\ g^{-1}$ muscle tissue: Ervik *et al.* 1994). In each case, mean concentrations for positive samples exceed the current European Union limits for these substances in skin and muscle of finfish for human consumption: oxytetracycline: 0.1 $\mu g\ g^{-1}$; oxolinic acid: 0.1 $\mu g\ g^{-1}$; flumequine: 0.6 $\mu g\ g^{-1}$ (European Union 2010). It should be noted that the development of new vaccines has allowed fish farmers in some areas (e.g. salmonid farms in Norway and Scotland) to largely cease antimicrobial use despite rapid expansion of the industry, but use remains high in other regions (Watts *et al.* 2017). It remains unclear whether antimicrobial residue impacts fitness in farm-associated wild fish, whether through toxicity, loss of gut microbiota or antimicrobial resistance in pathogens.

There have also been assessments of organohalogens and metals in the tissues of farm-associated wild fish. One study reported significantly higher levels of organochlorines and polybrominated diphenyl ethers in farm-associated fish relative to those from reference sites (1.5× higher in cod, 1.2× higher in saithe: Bustnes *et al.* 2010). Another reported higher levels (2.1×) of mercury in tissues of farm-associated rockfish (*Sebastes* spp.), potentially related to an increase in trophic level near farms (DeBruyn *et al.* 2006). In the most comprehensive study to date, Bustnes *et al.* (2011) measured concentrations of 30 elements in cod and saithe livers from three regions in Norway. In saithe, Hg (2.0×), U (1.4×), Cr (1.9×) and Mn (1.6×) concentrations were significantly higher in farm-associated fish, while Se, Zn, Cd, Cs and As were higher at reference sites. In cod, U (1.4×), Al (1.5×) and Ba (1.9×) were higher in farm-associated fish, while Se, Zn, Cd, Cs and As were higher at reference sites. While there is evidence that some metals accumulate in sediments under fish farms, there is little evidence so far that farm-associated wild fish are accumulating high concentrations in their tissues.

Infection rates

We discovered 22 studies that empirically investigated viral, bacterial or parasite transmission between farmed and wild populations. In all cases, the authors concluded that the risk of infection was either unchanged or elevated by interactions between farms and wild fish populations. Of the 11 studies that quantified changes in infection levels with the presence of active fish farms, all found higher levels of infection in farm-associated wild fish, with a mean 16× increase overall (RR = 2.1, t_{10} = 5.5, P = 0.0003). This large effect was primarily driven by eight studies of sea louse infection loads on wild salmonids near salmon farms (3.5–73× increase, RR = 2.5). One study reported higher infection densities of external parasites but lower densities of internal parasites in farm-associated gadids, probably as a result of consuming fewer infected wild fish and invertebrates in favour of commercial feed (Dempster *et al.* 2011). Three studies provided molecular evidence for likely viral or bacterial transmission between cultured and wild fish in the Mediterranean Sea (Zlotkin *et al.* 1998; Diamant *et al.* 2000; Colorni *et al.* 2002), and a molecular analysis of stomach contents revealed that wild cod consumed escaped salmon stock infected with piscine reovirus (Glover *et al.* 2013). However, molecular evidence did not always support the transmission hypothesis: Mladineo *et al.* (2009) reported that monogenean and isopod parasites were not transmitted between wild and farmed fish at one Mediterranean Sea farm.

Survivorship and fertility rates

Only two studies in our database estimated differential mortality rates in farm-associated fauna. Kilambi *et al.* (1978) used age structure to infer a 21% increase in survivorship of largemouth bass following the establishment of cage culture in a freshwater lake, while in contrast, Broyer *et al.* (2017) recorded 39% higher mortality of ducklings at fish ponds. In sea cage systems, elevated external parasitism rates (especially sea louse infections on salmonids) may increase mortality in farm-associated fish, but to our knowledge, differential mortality between farm and reference sites has not yet been empirically demonstrated. A further six studies quantified culling of numerous birds at farms but did not compare mortality rates at farms to those at reference sites. Two others reported dolphins being accidentally drowned in antipredator nets (Kemper & Gibbs 2001; Diaz López & Bernal-Shirai 2007), but again, did not benchmark these against natural mortality rates. Several studies noted higher fishing effort adjacent to sea cages, although we are only aware of two studies that quantified fishing effort and catch rates (Akyol & Ertosluk 2010; Bacher & Gordoa 2016), and none assessed fishing mortality rates among farm-associated fish.

Estimates of fertility (i.e. reproductive success) for wildlife at farms are similarly rare, but two recent examples were returned by our search, both documenting probable ecological traps: Kloskowski (2012) reported that fledging rates of grebes nesting on fish ponds stocked with +1 carp were only 37% of those nesting on unstocked ponds, while Broyer *et al.* (2017) found that high food availability was outweighed by high predation rates for ducks nesting on stocked ponds (Table 1).

Conflict with aquaculture operations

Birds were usually predators of stock. A total of 45 of 53 studies that documented interactions with birds considered predation on stock to be the major habitat use, whether in cages, ponds, shellfish beds or longlines. The most common avian predators were cormorants and herons. A total of 24 of 38 studies of interactions with wild mammals considered predation to be the major habitat use, in most cases by otters in ponds or sea cages (12 studies) or pinnipeds in sea cages (10 studies). Five studies reported herbivorous fishes inhabiting algae farms, but only one presented clear evidence of fish consuming algal crops (Anyango *et al.* 2017). One study reported predation of farmed mussels by wild fish (Segvic-Bubic *et al.* 2011), while three reported snakes taking stock from hatchery ponds (Plummer & Goy 1984; Gregory & Nelson 1991; Nelson & Gregory 2000).

Of the 77 studies that reported predation on stock or damage to infrastructure, only 11 quantified stock losses as a proportion of potential production, with a mean loss of 15% (range 0–50%). The lower end of that range was due to mammals taking only dead or moribund fish from hatcheries (Pitt & Conover 1996), while the upper was due to predation by cormorants in fish ponds (Barlow & Bock 1984). Other studies quantified consumption of stock by individual predators without placing it in the context of potential production (e.g. Glahn *et al.* 1999). In addition to predating stock, pinnipeds were reported to damage nets and cause fish escapes (e.g. Güçlüsoy & Savas 2003; Sepúlveda & Oliva 2005).

Discussion

Responses to aquaculture by wildlife vary greatly across taxonomic groups and culturing systems, but our systematic review and meta-analysis reveals several key and well-supported trends within taxonomic groups and culturing systems and identifies clear knowledge gaps to inform future research.

Are wildlife attracted to aquaculture?

Fish

Multiple lines of evidence suggest that many fish species prefer aquaculture sites over natural habitats, and on average, farms are associated with a much higher density and diversity of wild fish. The few available tracking studies indicate that farm-associated wild fish tend to be either residents or regular visitors (Otterå & Skilbrei 2014; Arechavala-Lopez *et al.* 2015a; Loiseau *et al.* 2016; Tsuyuki & Umino 2017), with spilled feed and waste likely to be the major attractive cues driving wild fish aggregations (Tuya *et al.* 2006; Bacher *et al.* 2015; Ballester-Moltó *et al.* 2015). Effects on fish abundance and diversity are also likely to depend on the functional group being assessed, with most surveys of fish populations at farms and reference sites targeting mobile generalist carnivores (either by design or through choice of sampling method).

Birds

Studies of bird abundance revealed highly variable responses to farms, but our meta-analysis indicates that aquaculture sites are associated with higher bird species richness overall. Numerous studies documented large bird populations at farms without comparing them to natural waterways, making it difficult to draw conclusions about the influence of farms on the spatial distribution of wildlife. Furthermore, little work has been done to assess responses at the individual level (i.e. migration or site fidelity) that can assist in inferring habitat preferences (Robertson & Hutto 2006), but it is likely that many bird species (especially herons, cormorants and gulls) find the availability of prey at fish and crustacean farms highly attractive (Barlow & Bock 1984; Stickley *et al.* 1992, 1995; Carss 1993; Glahn *et al.* 1999; Harrison 2009). Shellfish farms also increase local abundance of generalist or molluscivorous bird functional groups (Roycroft *et al.* 2004; Kirk *et al.* 2007), but others, such as invertivorous wading birds, may be displaced by shellfish farm infrastructure or associated ecological changes (Kelly *et al.* 1996; Godet *et al.* 2009; Broyer & Calenge 2010).

Mammals

Marine mammals (pinnipeds and dolphins) also showed highly variable responses to the presence of aquaculture, ranging from resident nuisance animals (Pemberton & Shaughnessy 1993; Hume *et al.* 2002; Güçlüsoy & Savas 2003; Sepúlveda & Oliva 2005) to periodic visitors (Diaz López 2012, 2017; Díaz López & Methion 2017), to active avoidance of farms (Markowitz *et al.* 2004; Watson-Capps & Mann 2005; Pearson 2009; Becker *et al.* 2011). Otters were common at freshwater fish ponds (Kloskowski 2005; Kortan *et al.* 2007) and estuarine sea cages in Europe (Freitas *et al.* 2007; Sales-Luis *et al.* 2009), but our search did not reveal any data on abundance or attraction to farms relative to natural waterways.

How does aquaculture affect fitness of wildlife?

Fish

Our meta-analysis indicated that farm-associated fish tend to be larger and heavier, a finding that is consistent with either aggregation of adult fish or higher growth rates due to a trophic subsidy. This larger average size, together with greater abundance overall, results in a very high local biomass of farm-associated wild fish. Despite this, farm-associated fish had similar or higher body condition metrics and rates of stomach fullness than fish from reference sites (Fernandez-Jover *et al.* 2007a; Dempster *et al.* 2011), indicating that farm environments may have a higher carrying capacity for wild fish than reference sites. However, any potential positive effects – such as higher reproductive potential – may be opposed by orders of magnitude higher infection loads near farms (especially sea lice on salmonids: Krkošek 2017) and possible impacts of a dietary shift from marine-derived to terrestrially derived fatty acids in commercial aquaculture feed (Lavens *et al.* 1999; Mazorra *et al.* 2003; Salze *et al.* 2005; Bogevik *et al.* 2012; Arechavala-Lopez *et al.* 2015b). Little is known about how the plurality of environmental changes at farms combines to influence survival and reproduction in wild fish. Mortality rates are difficult to measure directly, but Kilambi *et al.* (1978) compared age structure and recapture rates in a lake before and after the commencement of cage farming and inferred that survivorship had increased with farming.

In this study, we only assessed direct interactions between aquaculture activities and wildlife, but indirect interactions also occur, and are likely to have a considerable bearing on outcomes for fish populations in farming areas. Dietary shifts may occur indirectly via benthic nutrient loading and subsequent ecological changes across multiple trophic levels (Brown *et al.* 1987; Wu 1995; Yucel-Gier *et al.* 2007; White *et al.* 2017), and potential deleterious effects of direct or indirect dietary shifts or other changes may be most apparent in eggs or offspring of farm-associated fish (Salze *et al.* 2005; Barrett *et al.* 2018). Aggregations of large predators around sea cages may also reduce survivorship of fish that inhabit the same area (Güçlüsoy & Savas 2003). Fish that escape from farms can reduce fitness in native populations through disease transmission (Arechavala-López *et al.* 2013; Glover *et al.* 2013), genetic mixing (Glover *et al.* 2017), and interference with spawning or competition with offspring and adults (Jensen *et al.* 2010; Sundt-Hansen *et al.* 2015).

Birds

In birds, the effects of farm proximity on fitness are even less clear; only in a few cases were we able to extract usable data on direct or indirect fitness metrics. Numerous studies reported birds taking stock from ponds and cages, but none in our database compared feeding rates to those on natural waterways. Nonetheless, we expect food availability to be high provided that birds are able to access suitable food items (e.g. feed, stock or wild prey co-occurring at farms). However, predatory birds also experience high mortality from culling and antipredator net entanglements where such methods are employed, potentially causing fish farms to act as ecological traps for birds if mortality rates outweigh any benefits of higher food availability (Carss 1994; Belant *et al.* 2000; Blackwell *et al.* 2000; Bechard & Márquez-Reyes 2003; Quick *et al.* 2004). Negative effects will be exacerbated if food availability is lower than advertised, for example if piscivores are attracted to fish ponds but cannot access fish due to antipredator nets, or if stocking regimes lead to cohorts of fish that are too large to be consumed. This latter scenario was observed by Kloskowski (2012), who reported that European carp farms were acting as ecological traps for red-necked grebes, as farmed fish were too large for fledglings to consume leading to starvation. Predation risk for clutches may also be elevated at farms: Broyer *et al.* (2017) observed high densities of breeding pairs and high food availability, but also high offspring mortality – a probable ecological trap. Conversely, tuna ranching in Australia was associated with a population boom for silver gulls and appears to be a clear case of fish farms functioning as a strong population source for wildlife – reproductive success for the gulls was dramatically increased by the trophic subsidy obtained by exploiting farm feed (Harrison 2009). Similarly, long-term trends in wading bird populations closely tracked the scale of crayfish aquaculture in the southern United States (Fleury & Sherry 1995).

Mammals

Effects of aquaculture on mortality and reproduction of aquatic mammals are little known, but as with piscivorous birds, net effects are likely to depend on a trade-off between high food availability and high risk from culling and entanglements. Cetaceans may benefit from easy food when they visit farms (Diaz López 2017) and culling and entanglements are relatively rare (Diaz López & Bernal-Shirai 2007; Callier *et al.* 2017). As a result, attraction to farms may be an adaptive trait that results in increased fitness on balance, although we lack direct evidence for this. In contrast to cetaceans, pinnipeds experience heavy mortality from culling (Güçlüsoy & Savas 2003; Quick *et al.* 2004; Callier *et al.* 2017) and are more vulnerable to accidental entanglement (Callier *et al.* 2017). High mortality rates are likely to outweigh any increase in food availability for a long-lived, slow-breeding animal such that seals that are attracted to farms may be vulnerable to ecological traps driven by culling at farms.

Conflict and potential mutualism between aquaculture and wildlife

Our meta-analysis revealed that the nature of interactions between wild fauna and aquaculture was highly dependent on the taxon. Wild fish generally do not interact directly with stock unless small enough to enter sea cages through the mesh (although in rare cases wild fish may damage nets: Moe *et al.* 2007; Sanchez-Jerez *et al.* 2008). Of more concern is the role that wild populations play as reservoirs for pathogens and parasites, facilitating reinfection of farms (Uglem *et al.* 2014). This is an inevitable risk of farming in open systems, but research is underway to lower infection rates by minimising spatiotemporal overlap between stock and zones of high infection risk (Samsing *et al.* 2016;

Wright *et al.* 2017). Together with post-infection treatments, such measures also minimise the role that farms play as amplifiers of pathogen and parasite populations.

Most studies returned by our search concluded that predation or damage by birds and mammals is an ongoing problem for managers, but stock losses were rarely quantified (but see some recent examples: Sun *et al.* 2004; Sepúlveda & Oliva 2005; Morrison & Vogel 2009; Dorr *et al.* 2012). Where suitably habituated, pinnipeds have a propensity to become 'nuisance animals', damaging nets (leading to fish escapes) and consuming or stressing stock (Kemper *et al.* 2003; Quick *et al.* 2004; Sepúlveda & Oliva 2005). Such problems are difficult to solve. Culling is undesirable as it increases environmental impacts and negatively affects public perceptions of aquaculture. Relocation is expensive and often ineffective (Hume *et al.* 2002) and scaring devices have a limited effective lifespan before animals are desensitised. Exclusion using steel mesh appears to be the only viable option in some cases (Pemberton & Shaughnessy 1993).

While there tends to be a focus on negative interactions between farms and wild fauna, wild fish can provide ecosystem services to aquaculture operations by increasing animal welfare and reducing local environmental impacts of farming. Invertivorous fish that are small enough to gain access to sea cages (such as wrasse and lumpfish in Norwegian salmon farms) can act as cleaner fish and significantly reduce parasite loads on stock. Cleaner fish are now being deployed in large numbers for this purpose (Imsland *et al.* 2014; Skiftesvik *et al.* 2014). Wild fish and invertebrates ameliorate and disperse benthic nutrient loads by consuming spilled feed, faeces and dead stock (Vita *et al.* 2004; Felsing *et al.* 2005; Fernandez-Jover *et al.* 2007b). However, resident populations of large predators at fish farms may impede this waste amelioration service by scaring or consuming wild fish (Diaz López 2006), resulting in more severe benthic impacts, but such predators also prey on escaped fish, potentially reducing the risk of genetic introgression from farmed to wild fish populations (Glover *et al.* 2017).

For fish farming to continue to grow, farmers need to demonstrate environmental sustainability and good animal welfare standards. Protecting wild fish aggregations to take advantage of the ecosystem services they provide may be an important part of achieving these goals. Continued development of non-lethal bird and pinniped exclusion methods will be a necessary step.

Recommendations for future research on impacts of aquaculture on wildlife

Simply documenting behaviour of wildlife at farms or changes in wildlife abundance provides little information on the effects of aquaculture on persistence of wildlife populations. Aquaculture can have qualitatively distinct effects on wildlife that are superficially indistinguishable in the absence of data on habitat selection decisions, movement or fitness. For example, an elevated density of wildlife at a farm relative to a reference site may support various contradictory hypotheses, including but not limited to: (i) high survivorship or fertility causing the farm to function as a productive population source, with or without strong attraction, and typically with density-dependent spillover to surrounding areas (Pulliam 1988), or (ii) strong attraction to the farm habitat but high mortality rates or low reproductive success for residents. The latter scenario describes an attractive population sink (ecological trap) that draws animals in from surrounding areas and causes deleterious population effects disproportionate to its area (Hale *et al.* 2015). Our meta-analysis reveals that in most cases we do not have sufficient data on fitness outcomes, either direct or indirect, and as a result cannot distinguish between attractive or productive population effects, or their resultant positive or negative effects on wild populations.

Conceptual frameworks have been developed to distinguish between these two (non-mutually-exclusive) processes on artificial reefs and fish aggregation devices (Osenberg *et al.* 2002; Brickhill *et al.* 2005; Reubens *et al.* 2013) and may be applied to aquaculture sites. Evidence for attraction without significant production of wild fauna at aquaculture sites may include: (i) rarity of younger cohorts relative to older cohorts, (ii) population declines at adjacent reference sites corresponding to increases at farms, (iii) high mortality or reproductive failure rates at farms or (iv) tracking, microchemistry, tissue fatty acid or stable isotope analysis indicating recent immigration to farms. Conversely, evidence for high individual fitness leading to productive wild populations at farms may include, depending on the taxa: (i) successful breeding pairs residing at farms, (ii) high densities of larvae or juveniles, (iii) increases in abundance at farms followed by increases at adjacent reference sites consistent with density-dependent spillover, (iv) tracking, microchemistry, tissue fatty acid and stable isotope analysis indicating that most individuals are not recent immigrants.

Importantly, the above criteria for separating attraction and production are most relevant when compared to reference habitats (i.e. Is residing at a farm a good decision for an individual, or likely to lead to an ecological trap?). Only 91/204 studies included in our database allowed us to infer changes in at least one variable in farm-associated wildlife by making comparison to reference sites or timepoints. In many cases, changes in distribution or health of wildlife were not central to the study, but in other cases, there was a lost opportunity to understand more about these interactions. Where relevant, we recommend that studies of abundance or fitness of wild fauna at farms should benchmark their findings against reference sites or time-points (Underwood 1994; Osenberg *et al.* 2002; Brickhill *et al.* 2005). Reference sites should be appropriate for the hypotheses being tested. For example, our meta-analysis revealed that inferred increases in population densities at sea cage fish farms vary by orders of magnitude depending on whether the reference habitat is a nearby natural reef or featureless open water. Accordingly, researchers should be clear in their reasons for selecting a given reference habitat.

Most importantly, we have highlighted the paucity of data on mortality rates and reproductive success in farm-associated fauna. Such data are central to our understanding of the environmental impacts of aquaculture but can be difficult to obtain. Population-level metrics can be effective in closed or semi-closed systems (Kilambi *et al.* 1978), and researchers have long been capable of tracking mortality and breeding success in birds, including at aquaculture sites (Kloskowski 2012; Broyer *et al.* 2017). Open systems with highly mobile taxa (such as wild fish associated with sea cage aquaculture) present a greater challenge, but in coastal environments, acoustic tags in conjunction with external tags can provide excellent data on spatiotemporal movement and mortality rates in areas with differing levels of farm activity (Olsen & Moland 2011; Olsen *et al.* 2012; Fernández-Chacón *et al.* 2015).

It is now well established that wild fish are typically more abundant at sea cage fish farms than reference sites and that such fish are likely to consume farm waste, experience nutritional shifts and depending on the system, be exposed to elevated parasite loads. The challenge now is to develop an equivalent state of knowledge for other wild taxa and aquaculture systems and to obtain more direct measures of the effects of farm association on wildlife populations.

Data accessibility

See Appendix I for a full list of research articles included in this study.

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Appendix I
List of 191 articles included in systematic review and meta-analysis

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Summary of results for zero-inflated Poisson model comparing research effort on interactions between wildlife (number of articles included in our systematic review) and aquaculture between nations according to both domestic aquaculture production (t) in 2015 and Human Development Index (HDI) in 2015.

Table S2. List of the six most parsimonious linear models predicting log response ratios for wildlife abundance (a) and species richness (b) at aquaculture sites relative to reference sites.

Table S3. ANOVA table and Tukey's *post-hoc* test results (multiple comparisons of means with 95% family-wise confidence level) for best fitting linear model for factors predicting log response ratios (RR) for wildlife abundance at aquaculture sites.

Table S4. ANOVA table and Tukey's *post-hoc* test results for best fitting linear model for factors predicting log response ratios (RR) for wildlife species richness at aquaculture sites.