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More rapid and severe disease outbreaks for aquaculture at the tropics: implications for food security

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Summary

1. Aquaculture is replacing capture fisheries in supplying the world with dietary protein. Although disease is a major threat to aquaculture production, the underlying global epidemiological patterns are unknown.

2. We analysed disease outbreak severity across different latitudes in a diverse range of aquaculture systems.

3. Disease at lower latitudes progresses more rapidly and results in higher cumulative mortality, in particular at early stages of development and in shellfish.

4. Tropical countries suffer proportionally greater losses in aquaculture during disease outbreaks and have less time to mitigate losses.

5. *Synthesis and applications*. Disease can present a major problem for food production and security in equatorial regions where fish and shellfish provide a major source of dietary protein. As the incidences of some infectious diseases may increase with climate change, adaptation strategies must consider global patterns in disease vulnerability of aquaculture and develop options to minimize impacts on food production.

Key-words: climate change adaptation, disease, epidemiology, epizootics, latitudinal trend

Introduction

Food security is a pressing global issue as the human population is projected to reach between 7.5 and 10.5 billion by 2050 (UNPD 2006). With capture fisheries becoming increasingly unsustainable due to overfishing, aquaculture is expected to overtake capture fisheries in supplying the world's protein requirements in the future (FAO 2012). Indeed, aquaculture is the fastest growing food production sector in the world, with an average annual growth rate of 6.3% since 2000 (average 8.8% per year between 1980 and 2010) and currently accounts for approximately 47% of the world's fish supply (FAO 2012). Although the precise impacts and direction of climate-driven change for particular fish stocks and fisheries are uncertain, in countries which depend heavily upon fisheries for their livelihood, climate change is expected to result in increased economic hardship or missed opportunities for development (Allison *et al*. 2009). These countries are also the most vulnerable to the effects of climate change as they have the least capacity to implement adaptive actions (Dulvy *et al*. 2011). Aquaculture is expected to contribute to food security and improving the socio-economic status of developing countries (Godfray *et al*. 2010) and thus provide adaptive capacity to the effects of climate change and food shortages.

However, aquaculture may not be a panacea for food security. As in other forms of intensive and semi-intensive agriculture, infectious disease is a major problem. Waterborne pathogens can spread at faster rates than in terrestrial systems (McCallum, Harvell & Dobson 2003), and oceanographic transport processes have the potential to transmit disease across vast geographic regions, for example, pilchard herpesvirus was spread to >5000 km of Australian coastline at 30 km day^{-1} (Whittington *et al*. 1997). In fact, infectious disease is by far the biggest killer of farmed fishes (Pillay & Kutty 2005); an outbreak can often wipe out entire stocks, requiring costly decontamination of the associated facilities and equipment (Pillay &

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Kutty 2005), and has been identified as a potential limiting factor to aquaculture production (Jansen *et al.* 2012). The epidemiological issues associated with aquaculture will also be exacerbated by climate change (Karvonen *et al.* 2010). Extreme weather events are predicted to become more severe and more frequent in the future (IPCC 2007) favouring pathogen outbreaks following seasonal periods associated with changes in temperature and precipitation (Altizer *et al.* 2006). Additionally, increases in temperature are expected to lead to the introduction of pathogens to new regions by producing environmental conditions that favour pathogen growth and transmission (Harvell *et al.* 2002).

In spite of the expected issues with disease in aquaculture settings, the underlying global patterns in disease outbreaks have not been identified. However, in natural systems, the number of parasite or pathogen species infecting each host species tends to be higher at the lower latitudes (Rohde & Heap 1998; Guernier, Hochberg & Guegan 2004; Nunn *et al.* 2005), as well as reaching higher infection intensity (Calvete 2003; Benejam *et al.* 2009) and prevalence (Merino *et al.* 2008). Infectious disease–related mortalities are also more likely to occur at lower latitudes where relatively warmer climate promotes higher pathogen proliferation and transmission rates (Robar, Burness & Murray 2010). Thus, the ecological literature certainly suggests that similar patterns may be present in aquacultural systems, but this has not been investigated perhaps due to the assumption that such patterns will be mitigated by disease control measures. Establishing whether macroecological patterns of infectious disease are present in farmed settings can contribute valuable insights into the environmental drivers of diseases and appropriate management procedures for outbreaks. For example, ecological theories have facilitated the development and implementation of control measures for human infectious diseases and public health policies (Smith *et al.* 2005).

The potential for disease outbreak dynamics to be mediated by changes in climate and impact food production highlights the importance of establishing the current macroecological patterns of disease outbreaks in aquaculture at a global scale. Baseline epidemiological patterns will aid predictions of future outbreak patterns and contribute to building forward thinking aquaculture infrastructure and adaptive management strategies. Here, we analysed the epidemiological pattern of disease outbreaks in aquaculture across the globe (Fig. 1a) using data from published sources on disease outbreaks that have occurred in aquaculture facilities (see Table S1, Supporting information). We quantified the severity and duration of disease outbreaks across latitude for juvenile and adult stages of various fish and invertebrate species infected by viral, bacterial and parasitic disease-causing agents. Origin

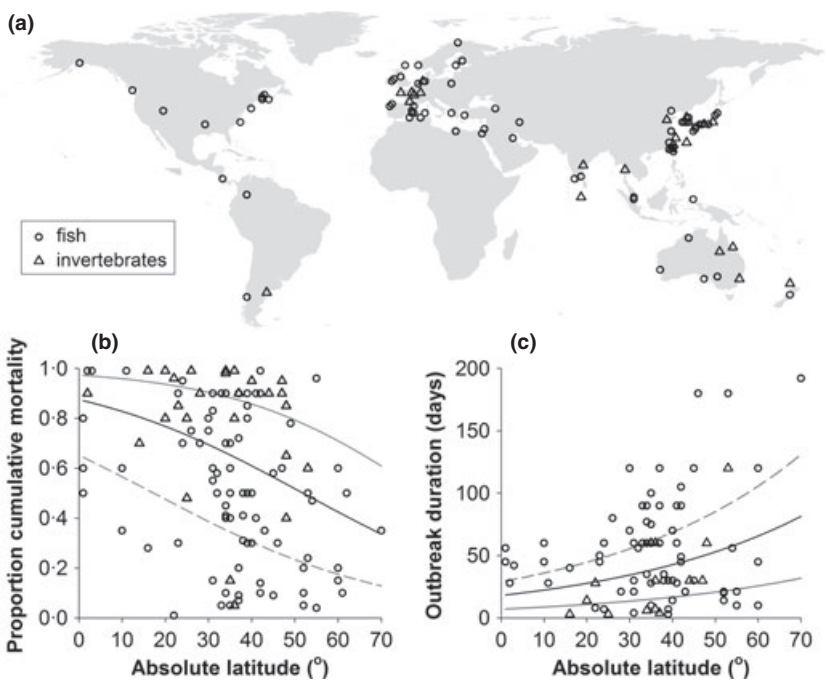

Fig. 1. Geographic distribution and severity of published disease outbreaks in aquaculture systems. (a) Locations of aquaculture-based disease events included in this study for fish and invertebrates. (b) Relationship between proportion cumulative mortality (total number of observations = 114) and absolute latitude resulting from disease outbreak. (c) Outbreak duration vs. absolute latitude (total number of observations = 91). Predicted relationships represent the grand mean (black line), adult fish cultured within their native range infected with a bacterial infection for total cumulative mortality, panel b, or a regional study scale, panel c (solid grey), and maximum cumulative mortality for juvenile invertebrates outside their native range with parasite infections for maximum cumulative mortality, panel b, or a local study scale, panel c (dotted grey). Predicted values are for a government efficiency index of 0.

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and life stage of each host were additional explanatory factors. To account for variation in veterinary and disease reporting infrastructure, which is expected to differ between countries, we also included an index of governance efficiency that considers the quality of policy formation and implementation among other aspects of governance (The World Bank Group 2011). Finally, because cumulative mortality was reported as either a total or a maximum value and outbreak duration was for either local (e.g. tank, pond, net, single site) or regional scales (e.g. multiple farms), we also included those information as factors.

Materials and methods

DATA COLLECTION AND INCLUSION CRITERIA

We gathered data from published reports from peer-reviewed publications of disease-induced mortalities in commercial aquaculture facilities. All relevant studies available to either author were obtained by browsing all issues in relevant peer-reviewed journals as of 15 June 2011 (see Table S1). Additional literature searches were conducted using ISI Web of Knowledge and Google Scholar using a combination of search term 'Aquacult*' AND 'Outbreak' OR 'Epizootic' OR 'Epidemic' OR 'Mortalit*'. Studies reporting on the severity (number or percentage of mortalities) and/or duration of the outbreak were selected. From this set, any studies reporting intervention action that lead to significant change in mortality parameters were excluded.

Where possible, we obtained the following information from each study: maximum cumulative mortality, duration of the outbreak, latitude and longitude of outbreak location, aquaculture species, life stage, host origin and pathogen type (Table S1). We also searched for additional parameters (stocking density, rearing method, water temperature and time of year in which the outbreak occurred), but these factors were not included because we could not obtain complete data (Table S1). Disease outbreaks at larval stages, which show the same trends as adult and juveniles, tended to result in cumulative mortality >80%. However, because of low sample size, larval outbreak data are not included in analyses but appear in Table S1.

Each entry in our data set corresponds to one aquaculture species at a particular location over a single continuous period of time. Separate entries were included for each species in studies that reported mortality in more than one aquaculture species. Where multiple levels of cumulative mortalities were reported, only the maximum cumulative mortality was recorded. Pathogens were identified as a virus, bacterium or parasite. Parasites are defined as eukaryotic parasitic organisms including fungi, microsporidians, protozoans, dinoflagellates, myxosporeans, arthropods, platyhelminths and nematodes.

STATISTICAL METHODS

We quantified the relationships between outbreak mortality and duration with absolute latitude using Linear and Generalized Linear Modelling approaches. We started with a full set of explanatory factors as fixed effects based on *a priori* hypotheses which data were available: life stage (adult vs. juvenile), taxon (fish vs. invertebrate), agent (bacterium vs. parasite vs. virus) and host origin (non-native vs. native host). We further included government effectiveness (defined as 'perceptions of the quality of public services, the quality of the civil service and the degree of its independence from political pressures, the quality of policy formulation and implementation, and the credibility of the government's commitment to such policies'– (The World Bank Group 2011) as an indicator of governance efficiency due to the potential issue of latitudinal trends being driven by disease reporting quality (Fig. 2). Mortality metric (total vs. maximum) and study scale (local vs. regional) were also included for the responses, respectively, cumulative mortality and outbreak duration. Nested taxonomy (family/genus/species) was included as a random effect on the model intercept to account for variation in the response variable due to multiple reports of related taxa. Collinearity diagnostics (Zuur, Ieno & Elphick 2009) were performed by quantifying generalized variance inflation factors (GVIF) for each fixed factor and interactions with latitude (latitude was centred prior to the analysis) using the function *preds. GVIF* available through the R (R Development Core Team 2011) package 'car' (Fox & Weisberg 2011). We removed interaction terms with latitude from our full model because GVIF values exceeded the arbitrary threshold of 2. The interaction between latitude and taxon was excluded because the majority of outbreak data (*c.* 80%) were from fish.

Model selection consisted of comparing fixed- and mixed-effects models. This allowed us to assess whether including nested taxonomic levels as random effects was justified by examining the variance component explained by family, genus and species. Because the variance that could be attributed to each taxonomic level was less than 0.0001% of the overall variance, we selected among possible fixed-effects models (glm with binomial or negative binomial error structure vs. lm following transformation of the response variable), as appropriate for proportion (cumulative mortality) and count (outbreak duration) data on the basis of graphical residual analysis.

Multimodel inference produced model-averaged parameter estimates and unconditional errors using AICc for all factors included in the full model (see Tables S2, Supporting information). The candidate model set included all possible combinations

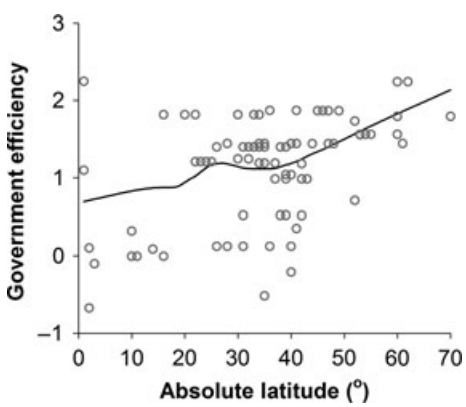

Fig. 2. Index of government effectiveness (World Bank Governance Indicator: The World Bank Group 2011, 'government effectiveness') vs. absolute latitude for the countries with disease outbreak reports included in Table S1. A loess smoothing curve (black line) indicates a positive relationship. Note that when latitude was removed from the model, the 95% confidence interval for government efficiency did not cross zero.

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of factors (note that interactions were not included). The confidence model set included models within a 90% confidence threshold (summed weight using AICc: Burnham & Anderson 2002) with the package 'MuMIn' (Bartoń 2009) and the function *model.avg* (missing coefficients were set to zero).

Results

We found that outbreak severity (in terms of cumulative mortality) was relatively higher in the tropics where outbreaks lead to an average cumulative mortality of 88% at the equator (Fig. 1b) and declined in temperate systems to 34% at 70° absolute latitude (Table 1a). Juvenile invertebrates were relatively more vulnerable in comparison with adult finfish, where at the equator, proportion cumulative mortality was, respectively, 0.96 vs. 0.65 (back-transformed parameter estimates where additional fixed factors and covariates equalled the reference: Table 1a). Disease outbreaks also proceeded more rapidly in the tropics; maximum outbreak duration at the equator was 60 days, whereas outbreaks in temperate regions were reported over durations of up to 192 days (Fig. 1c). Invertebrates tended to suffer more rapid disease progression than adult fish, with equatorial outbreaks lasting on average 15 vs. 30 days (back-transformed parameter estimates where additional fixed factors and covariates equalled the reference: Table 1b).

Table 1. Multimodel inference produced model-averaged parameter estimates, unconditional standard errors (SEu) and 95% confidence interval based on AICc for all factors included in the full model. (a) Cumulative mortality (Linear Model with logit-transformed response data) and (b) outbreak duration (Generalized Linear Model with a negative binomial error structure) as a function of two covariates: absolute latitude and governance efficiency and five factors: life stage (juvenile/*adult*), taxon (invertebrate/*fish*), origin (non-native/*native*), agent (parasite/virus/*bacterium*) and, for respectively, cumulative mortality and outbreak duration, mortality metric (maximum/*total*) and study scale (local/*regional*). The parameter estimate for 'reference' represents adult fish cultured within their native range and infected with a bacterium and, as appropriate for the response, values representing total cumulative mortality or a regional study scale (italicized above). Effect types are slope (shaded) and intercept (unshaded). Stars (*) indicate coefficients where the 95% CI does not cross zero

(a) Mortality

Fixed effects	Estimate	SEu	2.5%	97.5%
Reference	0.62	0.51	−0.39	1.63
Latitude*	−0.036	0.011	−0.057	−0.015
Governance efficiency	−0.11	0.25	−0.61	0.39
Life stage (juvenile)*	1.11	0.30	0.52	1.70
Taxon (invertebrate)*	1.38	0.34	0.69	2.06
Host origin (non-native)	0.34	0.35	−0.34	1.01
Agent (parasite)	0.14	0.37	−0.59	0.88
Agent (virus)	0.15	0.35	−0.54	0.85
Mortality metric (maximum)	0.55	0.32	−0.089	1.18

(b) Duration

Fixed effects	Coefficient	SEu	2.5%	97.5%
Reference	3.39	0.33	2.75	4.05
Latitude*	0.021	0.0062	0.0092	0.034
Governance efficiency	0.061	0.15	−0.25	0.36
Life stage (juvenile)	−0.060	0.17	−0.40	0.28
Taxon (invertebrate)*	−0.68	0.22	−1.12	−0.25
Host origin (non-native)	0.37	0.19	0.0054	−0.75
Agent (parasite)	−0.29	0.20	−0.69	0.11
Agent (virus)	0.025	0.20	−0.37	0.43
Study scale (local)	−0.10	0.16	−0.42	0.22

Discussion

The latitudinal trend in disease outbreak severity and duration may in part be explained by human factors such as the effectiveness of management practices, policy implementation and reporting infrastructure. There may be better fish disease monitoring and control measures available for countries at higher latitudes, and indeed, government efficiency correlated positively with latitude (Fig. 2). However, government efficiency did not show a significant relationship with outbreak characteristics (Table 1), even when latitude was removed as a model covariate (see Table S3, Supporting information). Moreover, these trends cannot be explained by different management practices and disease control capacity in different regions because we excluded studies where intervention ended an outbreak or reduced its severity.

Overall, our findings indicate that the increase in aquaculture disease impacts towards the tropics is likely to be driven (at least in part) by environmental factors. In natural systems, infectious disease–related mortality is also more likely to occur at lower latitudes where relatively warmer climate promotes higher pathogen proliferation and transmission rate (Robar, Burness and Murray 2010). Here, we demonstrate that this trend similarly applies to aquaculture populations. When combined with the crowded conditions of aquaculture facilities and warmer temperatures, this provides ideal conditions for outbreaks (Krkosek 2010; Mennerat *et al.* 2010; Salama & Murray 2011) that can lead to more severe mortality and rapid progression of diseases. Additionally in the last 50 years, lower latitudinal regions have also seen the greatest increase in nitrogen deposition (McKenzie & Townsend 2007). Higher nutrient loading is associated with increased risk of infectious diseases, for instance, nitrogenous compounds present in run-off can challenge host immune responses and promote pathogen replication rate (Martin *et al.* 2010). Thus, future research should seek to identify the environmental parameters and management system parameters at lower latitudes, which contribute to the pattern of higher mortality and rapid disease progression associated with epizootics.

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IMPLICATIONS FOR MANAGEMENT

The role of disease in limiting the aquaculture-based production of fish and shellfish has not been considered in empirical calculations of regional vulnerability to climate change (Handisyde *et al.* 2009). An important implication of our findings is that the aquaculture industry will need to focus on building the capacity to minimize and recover from pathogen-induced loss, an issue of greatest priority in tropical regions. There are different management approaches to minimizing vulnerabilities in aquaculture, such as investing in environmental monitoring infrastructure and steering towards sustainable production (Bush *et al.* 2010). Even so, any management framework should also take into account economic losses from disease outbreak (Karim *et al.* 2012). While aquaculture is considered a viable means to promote food security and improve socio-economic status of developing countries (Godfray *et al.* 2010), lower latitudinal regions have also been identified as being most vulnerable to the effects of climate change (Dulvy *et al.* 2011). Environmental change is expected to reduce available agricultural land and crop yield at lower latitudinal regions (Schmidhuber & Tubiello 2007) in additional to the productivity of capture fisheries (Cheung *et al.* 2010). Combined with the region's heavy dependency on fish protein (Allison *et al.* 2009; Dulvy *et al.* 2011) and the fact that 90% of the world's aquaculture production comes from developing countries (FAO 2012), our data present a strong case for considering the potential impacts of disease outbreaks in strategies to build infrastructure for food security in developing nations as a global priority.

Our results also suggest further directions for management consideration. For instance, juvenile stages displayed higher levels of disease-induced mortality than adults (Table 1a). This may be because the immune system of juveniles is not as fully developed compared with mature individuals. Additionally, juvenile stages have fewer resources to draw from to mount an effective response to infection without compromising other functions necessary for survival; thus, strategies to minimize mortality at juvenile stages will be important. We also found a general trend of higher mortality and shorter outbreak duration in invertebrates compared to finfish (Table 1). As invertebrates account for 35% of the world's total aquaculture production by volume (FAO 2012), mostly from low latitudinal regions (particularly crustaceans) (FAO 2010), research contributing to building disease resilience in shrimp and shellfish culture will be of primary importance to protecting food and socio-economic security.

FUTURE OF DISEASE OUTBREAKS IN AQUACULTURE

Aquaculture in tropical regions has the potential for greater economic loss in comparison with temperate regions due to climate change–mediated disease mortality in the light of current forecasts of decreasing water quality and supply and increasing frequency of extreme weather events (Handisyde *et al.* 2009). Moreover, environmental deterioration may be more severe in tropical nations and interact with climate change outcomes, which are predicted to increase the frequency and risk of disease (Harvell *et al.* 2002), as well as altering the distribution and severity of disease outbreaks (Rohr *et al.* 2011). It will be important to monitor such emerging trends to implement adaptive management strategies as climatic and nutrient deposition patterns may act synergistically to result in even greater frequency of disease-induced stock mortalities in aquaculture.

There are also important ecological ramifications associated with our findings that should be considered in future risk assessments. Aquaculture operations may be an increasing threat to wild stocks, a problem that may be global in scope and particularly so in tropical nations if disease is not considered in the implementation of open aquaculture facilities. Certain rearing methods, such as cage systems in marine or freshwater systems, can facilitate pathogen exchange between farmed and wild populations (Johansen *et al.* 2011), leading to pathogen spillover (Krkosek *et al.* 2006) or spillback (Kelly *et al.* 2009). As well as reducing the profitability and sustainability of farming (Salama & Murray 2011; Jansen *et al.* 2012), pathogen exchange can result in epizootics that threaten a range of wild species, a phenomenon that has been well documented from terrestrial systems (Gottdenker *et al.* 2005; Colla *et al.* 2006). Aquacultural settings also have the potential to select for the evolution of more virulent pathogens (Pulkkinen *et al.* 2010; Mennerat *et al.* 2012). The introduction of such pathogens into the surrounding environment via introduced aquaculture species can consequently have devastating impacts on wild fish populations and pose a significant threat to local biodiversity, especially to those species that may be facing a range of threats or occur at low population numbers (e.g. Gozlan *et al.* 2005). Coupled with our findings that more severe outbreaks occur at lower latitudinal regions – where biodiversity reaches a maximum (Gaston 2000) – makes the exchange and potential amplification of disease between farmed and nature populations a considerable concern not only for aquaculture sustainability but also its impact on local aquatic fauna and ecosystems. The risk of acquiring or introducing virulent pathogen to biologically diverse locations should be taken into consideration when selecting sites for aquaculture, thus making biosecurity a key consideration for aquaculture sustainability (Pruder 2004; Lightner 2005; Bush *et al.* 2010).

While aquaculture systems are typically considered 'artificial', the insights gained from studying natural host–parasite systems may have application to outbreaks in aquaculture and in particular where ranching strategies are used. While ecological approaches can be applied to facilitate the development of more effective disease control and management practices, studying disease outbreaks in aquaculture can also broaden our understanding

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of disease ecology. For example, research in aquaculture has revealed knowledge gaps in certain aspects of disease ecology such as immunology of invertebrates and its interactions with environmental factors (Mydlarz, Jones & Harvell 2006). Aquacultural systems provide a setting from which disease can be observed and documented in greater detail than outbreaks in the wild. Understanding how outbreaks are initiated and unfold in such settings can further provide insights into the evolutionary ecology of infectious agents, and there is a need for disease ecologists to engage and collaborate with members of aquaculture community.

RECOMMENDATIONS

Aquaculture operations at lower latitudes suffer higher cumulative mortality and faster outbreak progression, which in turn may be exacerbated by climate change, leading to conditions that select for more virulent pathogens (Mennerat *et al.* 2010). This can result in the introduction of pathogens with greater virulence into wild fisheries, a pattern well documented in terrestrial systems (Gottdenker *et al.* 2005; Colla *et al.* 2006). Identifying the environmental mechanisms underlying the relationship between latitude and outbreak severity and epizootic duration will be a fundamental direction for future research (Fig. 3).

Our review of the literature also revealed that many critical details required for in-depth global scale analyses of disease outbreaks often go unreported. Thus, there is a need to standardize the reporting of aquaculture-based epizootics to include key details such as sample size, duration, holding facility conditions, likely contributing factors (apart from the pathogenic agent itself), stocking density, rearing method, water temperature and time of year in which the outbreak occurred (Fig. 3). The requirement of detailed reports on outbreaks serves to highlight the importance of engaging with the aquaculture industry to encourage monitoring and reporting.

Identifying host traits and relative susceptibility to different disease agents under different conditions will be important to generate adaptation strategies that reduce the exposure of farmed animals to extreme climate conditions that stress physiological and immune systems (e.g. by moving net cages to depth when warm weather events are forecasted) and the sensitivity of animals to such exposure (e.g. through selection of thermotolerant genotypes for cultivation). Moreover, preventative actions are required to minimize the potential for common outbreak drivers such as high stock density, injuries following transport, closed rearing methods and open exchange pathways that lead to infection and spread (Bush *et al.* 2010; Salama & Murray 2011). By limiting the potential for disease outbreaks in combination with efforts to promote adaptive capacity, such as building the required expertise and infrastructure to farm species that are less susceptible to infection under climate change, will reduce the vulnerability of the industry to disease-related economic loss and adaptation efforts (Fig. 3).

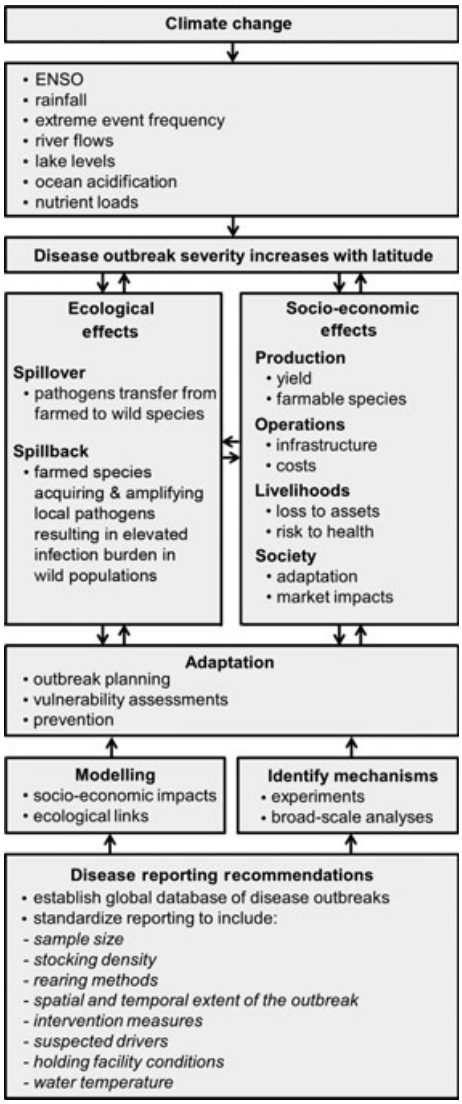

Fig. 3. Summary of linkages between the biophysical and socio-economic systems with disease outbreaks in aquaculture. Arrows indicate the direction of influence between those climate change–related physical factors expected to alter disease outbreak patterns in aquaculture and the ecological and socio-economic effects of outbreaks. We offer recommendations for reporting to inform both mechanistic understanding of disease outbreak patterns and forecasting capacity that will ultimately enhance adaptation efforts.

Our study indicates that, for aquaculture to become a viable and sustainable option for ensuring food security, particularly in developing countries, any such venture must be integrated with the development of reliable disease management plans and biosecurity infrastructure to promote outbreak prevention and resilience in production systems.

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T.L.F.L. and A.E.B. conceived the study, designed the experiment and collected the data. A.E.B. conducted the statistical analyses. T.L.F.L and A.E.B. discussed the results and wrote the manuscript.

The authors declare no competing financial interests.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Data table and references.

Table S2. Confidence model sets.

Table S3. Summary of model results with latitude removed as a covariate.

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