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Boom-and-bust production cycles in animal seafood aquaculture

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Abstract

Although aquaculture has grown nearly exponentially over the last six decades, providing 31.6 million metric tons of animal seafood in 2015, its rate of growth has slowed over the last 15 years. Here, we use case studies, drawn mostly from Asian shellfish culture, to suggest that 'boom-and-bust' production cycles – periods of rapid growth followed by collapse – cause significant losses of seafood production and to illustrate the duration and repetition of boom-and-bust cycles. Next, using the global FAO database for aquaculture production from 1950 to 2015, we investigate whether boom-and-bust cycles occur more broadly and whether they are playing a role in the declining rate of global aquaculture production. Focusing on FAO production records with maxima before 2011, allowing time for collapse, we categorize production in each record, relative to its maximum value, as sustained, depleted, collapsed or lost. We find 278 of 453 records (61.4%) show collapsed or lost production, although production in most of these records comprises only a tiny fraction of global output. The top 30 records in the collapsed or lost categories do account for 2.4% of cumulative production over the 66-year record of animal seafood aquaculture. We identify a strong association between short boom phases (5 years or less) and the probability that production will be lost and use this, as well as maximum annual production and year of maximum production, to model the probability of loss. Ecological limits and market problems are the most often discussed causes of boom-and-bust production cycles, but we focus, here, on disease as a major proximal cause of collapse and raise the hypothesis that inbreeding depression may often be an ultimate cause by exacerbating disease susceptibility.

Key words: biodiversity, disease, inbreeding depression, marine and brackish water, sequential collapses.

Introduction

Aquaculture is one of the fastest growing sectors of food production for human consumption. Since 1950, global aquaculture production has grown at a compound annual rate of 8.2%, although this rate has slowed to 6.2% over the past 15 years (FAO 2016, Zhou 2017). Still, in 2013, annual aquaculture production exceeded capture fishery landings (FAO 2016). In 2015, global aquaculture production attained 106 million metric tons (Mt), comprising 29.4 Mt of aquatic plants and 76.6 Mt of aquatic animals. Production of farmed fish, molluscs and crustaceans – 51.9, 16.4 and 7.4 Mt, respectively – accounted for 98.8% of aquatic animal production in 2015, but fish farmed in freshwater environments contributed 44.1 Mt to this total (FAO 2017). For reasons discussed in Methods, we focus in this review on animal 'seafood' aquaculture, the farming of molluscs and crustaceans and fish reared in marine or brackish-water environments (including freshwater species, such as tilapia, trout, freshwater mussels and clams and crayfish and river prawns), which produced 31.6 Mt in 2015.

Although global aquaculture production continues to increase, constraints are apparent (Bacher *et al.* 1991;

Troell *et al.* 2009; Burkholder & Shumway 2011). Diseases, in particular, are clearly increasing in major cultured fish and shellfish species around the world (Blaylock & Bullard 2014; Lafferty *et al.* 2015; FAO 2016; Guo & Ford 2016; Morash & Alter 2016; Pernet *et al.* 2016; Thitamadee *et al.* 2016) and have already caused massive losses of major farmed molluscs and crustaceans (Table 1). Viral, bacterial and protozoan pathogens are the identified causes in many cases, but causative agents sometimes remain elusive. At the level of individual cultured species and especially on national or regional levels, production varies considerably. Certain economically important mollusc and marine shrimp species exhibit classic, 'boom-and-bust' production cycles, in which a rapid increase in production leads to a similarly rapid collapse, owing typically to diseases or other stresses. When 'busts' occur, culture often shifts to alternative species, which may themselves enter into boom-and-bust production cycles. Several authors (Kautsky *et al.* 2000; Arquitt *et al.* 2005; Prusty *et al.* 2014) have previously noted and analysed boom-to-bust cycles in shrimp aquaculture. We present our initial observations of boom-and-bust production cycles in Asian shellfish culture as case studies motivating this review and illustrating general features of these cycles. The purpose of this review is to examine whether boom-and-bust cycles occur more broadly in the FAO global aquaculture production database (FAO 2017). The extent and impact of boom-and-bust production cycles in animal seafood aquaculture are important questions, because extensive exploitation of wild stocks for artificial propagation and escapes of hatchery-propagated stocks into the wild (Bondad-Reantaso *et al.* 2005) may pose a threat to marine biodiversity in general.

We analyse global aquaculture production statistics (FAO 2017) to see how common boom-and-bust production cycles are, to estimate the timescales involved and to assess the impact of boom-and-bust production on the growth of global seafood aquaculture. We find that short boom phases are associated with a significant probability of extirpation. Finally, we discuss causes of boom-and-bust production cycles. While acknowledging the roles of social, economic and environmental factors, we focus on disease as a major proximal cause of collapse. Following Doyle (2016), we further suggest the hypothesis that inbreeding depression, brought about by poor management of genetic resources in highly fecund aquatic species, exacerbates disease susceptibility and may thus be a significant ultimate cause of boom-and-bust production cycles.

Methods

Case studies

The genesis of this review was personal knowledge (by WWY) of important boom-and-bust production cycles, mostly in Asian shellfish aquaculture, which were not evident in FAO databases on global aquaculture production. We present these as case studies to illustrate features of boom-and-bust production cycles, such as duration and species replacements, as well as to summarize information about their causes from diseases. We obtained data on Chinese aquaculture production from the China Fisheries Statistics Yearbook (1985–2016) of the Fisheries Bureau, Ministry of Agriculture, People's Republic of China, which provides detailed information for species and provinces. The FAO database, as we show in Results, aggregates some of these data; for example, the molluscan database aggregates data on Chinese production of abalones and of scallops, under the Aquatic Sciences and Fisheries Information System (ASFIS) common names 'Abalones nei' (nei, not elsewhere included; ASFIS scientific name '*Haliotus* spp') and 'Scallops nei' (ASFIS scientific name Pectinidae), respectively.

Global production statistics

We used the FAO program FishStatJ 3.02.0 and the aquaculture production database released in March 2017, which has global data on quantity in metric tons (t) compiled annually for 1950 through 2015. FAO data provide an admittedly incomplete and inaccurate picture of global aquaculture (New 2017; Zhou 2017), but we focus on individual production records for particular species in particular countries rather than on global or regional aggregated production levels. Nevertheless, as detailed below, we do uncover and attempt to correct for some apparent errors in individual records.

We exclude fish grown in freshwater environments from consideration, despite preliminary findings that the overall occurrence and pattern of boom-and-bust production cycles in these records are similar to what we report here for fish reared in marine or brackish-water environments or for molluscs or crustaceans. However, inclusion of freshwater fish could bias analyses of causes and consequences of boom-and-bust cycles in seafood production for several reasons. First, the number of records for freshwater fish, over 1500, was greater than the combined number of records (1380) for fish reared in marine or brackish water, molluscs and crustaceans. Second, 10 species of carp dominate the freshwater records, accounting for more than a third of cumulative global production of all fish from 1950 to 2015. Third, the top producing freshwater fish species, mainly carps, have long histories of domestication, while most marine or brackish-water aquaculture species are proto-domesticates or exploited captives (Hedgecock 2012). Combining histories of domestication with an adaptive immune system, farmed freshwater fish are likely to have evolved adaptations to intensification and diseases so

Table 1 Losses from disease in some dominant cultured molluscs and prawn stocks

Species	Country or area	Year culture began	Year of peak production	Year when disease happened	Per cent lost production (%)	Pathogeny	Sources
Ostrea edulis	Arcachon, Marennes, France	1852	1912	1920	100	Unexplained mass mortality	Buestel *et al.* (2009)
Ostrea edulis	Brittany, France	1930	1960	1968	90	Protozoan, parasite	Buestel *et al.* (2009)
Crassostrea angulata	France	1860	1950	1966	100	Gill disease, viral disease	Comps and Duthoit (1976) and Comps *et al.* (1976)
Crassostrea gigas	France	1973	1996	2008	40	*OsHV-1* virus	Le Deuff and Renault (1999)
Crassostrea gigas	New Zealand	1970s	1999	2000s	90	*OsHV-1* virus	Webb *et al.* (2007)
Haliotis discus hannai	Northern China	1983	1992	1994	60	*Vibrio*	Zhang *et al.* (2004)
Haliotis diversicolor	Southern China	1992	2002	2003	95	*Vibrio*, Virus	Cai *et al.* (2006) and Zhang *et al.* (2004)
Haliotis diversicolor	Taiwan	1970s	2000	2003	95	*Vibrio*, Virus	Chang *et al.* (2005, 2008)
Chlamys farreri	Shandong, China	1983	1996	1997	80	Virus	Xiao *et al.* (2005)
Pinctada fucata	Japan	1970s	1993	1994	75	Parasites, virus, bacteria	Bondad-Reantaso *et al.* (2007) and Miyazaki *et al.* (1999)
Pinctada fucata	China	1980s	2006	2007	60	Parasites, bacteria	Bondad-Reantaso *et al.* (2007)
Fenneropenaeus chinensis	China	1980s	1991	1993	80	Virus	Zhan *et al.* (1998)
Macrobrachium rosenbergii	India	1989–1996	2005	2006	85	*Vibrio*, Virus	Pillai and Bonami (2012)
Penaeus monodon	Taiwan	1970s	1987	1988	95	Virus	Liao (1992)
Penaeus monodon	Thailand	1980s	2000	2001	95	Virus	Flegel (1997)

far lacking in their marine and brackish-water counterparts (Vazquez *et al.* 2009; Uribe *et al.* 2011; Guo & Ford 2016). Fourth, the fecundity of top freshwater aquaculture species is lower than the fecundity of most marine fish and shellfish by one or two orders of magnitude (Winemiller & Rose 1992), which could systematically affect population genetic parameters and processes (Hedgecock & Pudovkin 2011; Plough *et al.* 2016).

We used FAO database records for species of molluscs or crustaceans in a particular country aggregated over area and environment. For fish, we filtered, under species, 'Diadromous fishes', 'Freshwater fishes' and 'Marine fishes' and, under environment, 'Marine' and 'Brackish water' (718 records with nonzero cumulative production across the 1950–2015 interval; for purposes of this review, we consider freshwater fish reared in marine or brackish-water environments as 'seafood'). We exported the filtered records, separately, for 'Molluscs' (340 records with nonzero cumulative production across the interval) and for 'Crustaceans' (322 records with nonzero cumulative production across the interval). We imported records for these groups into three separate Excel 2016 spreadsheets for further analyses.

For the fish database, we combined unambiguous species records for countries that broke apart (the Socialist Federal Republic of Yugoslavia and the Union of Soviet Socialist Republics) with records for those same species in their daughter states, to obtain continuous records over the 1950–2015 interval. We kept, as separate records, production by daughter states of species not evidently produced by parent states. These changes resulted in a final database of 714 records. In crustacean records from India, we noticed aggregated records for marine prawns (*Penaeus* spp) and river prawns (*Macrobrachium* spp) in 2010, with zero production for individual species in these genera, which had data in preceding and subsequent years. To prevent misclassification of the status of the individual species, we estimated their 2010 production by interpolating between their 2009 and 2011 data, finding the relative proportional production of each species and multiplying this by the relevant aggregated sum. In all three spreadsheets, we visualized temporal patterns of production, using sparklines, data-intense, word-sized graphics (Tufte 2006), which facilitated identification of the data errors noted above, and of the trends and categories described in this review.

From each record of production, we extracted the year of maximum production (MXYR) and maximum annual production (MAX) and calculated cumulative production across all years. We then filtered the database to exclude minor records from downstream analyses, as these contributed little to global cumulative production and inspection of sparklines for these minor records suggested that their inclusion would bias upwards the number of boom-and-bust production cycles. For fish reared in marine and brackish-water environments, which had a cumulative production of 108.2 million metric tons (Mt) over the 66-year database, we used a threshold of cumulative production greater than or equal to 1000 t, which yielded 330 records. For molluscs, which had a cumulative production of 329.3 Mt, we used a threshold greater than or equal to 1000 t, which yielded 180 records. For crustaceans, which had a cumulative production of 88.6 Mt, we used a threshold greater than or equal to 300 t, which coincidentally yielded 180 records. The records retained by these criteria accounted for 99.9% or more of the cumulative production for each group.

We provisionally classified the *status* of each production record into four categories: (i) *sustained*, if production in any year following the peak or maximum level never dipped below 50% of the peak; (ii) *depleted*, if production dipped below 50% but stayed at or above 10% of the peak level; (iii) *collapsed*, if production dipped below 10% of the peak but never reached zero; and (iv) *lost*, if production reached zero in any year after peak production. Note that lost production may recover in a subsequent year. These categories of production status are arbitrary, though similar to those used in fisheries analyses (Worm *et al.* 2006, 2009) and mutually exclusive, such that depleted records do not subsequently collapse or go extinct and collapsed records do not go extinct. Lost records, of course, pass through the depleted and collapsed stages but are not included in those categories.

From each record, we extracted the year, in which each relevant level of status was achieved, and then determined the lengths of up to five intervals for each record, depending on status: (i) T_{peak}, the 'boom' phase, the number of years from the year in which production first reached 10% or more of MAX to MXYR; (ii) $T_{0.5}$, the number of years from MXYR to depleted production (50% of MAX); (iii) $T_{0.1}$, the number of years from MXYR to collapsed production (10% of MAX); (iv) T_0, the number of years from MXYR to loss; and (v) T_{b2b}, the sum of T_{peak} and $T_{0.1}$ for a given record, that is the number of years from the start of a boom in production to its bust (collapse). As the lengths of boom-and-bust intervals have non-normal, often L-shaped distributions and unequal variances, we use nonparametric statistics as implemented in the SAS 9.4 procedure NPAR1-WAY to compare the locations and shapes of these distributions for the class variable, status. We compared two samples using the asymptotic Kolmogorov–Smirnoff test (KSa); when comparing multiple samples, we used the Kruskal–Wallis test for Wilcoxon scores (rank sums), with *P*-value computed from the asymptotic chi-square

Table 2 Summary statistics on the status of aquaculture records with peak production before 2011

Record status	Number of records	Per cent of records (%)	Per cent of cumulative production (%)	Average $CV_{Start\text{-}2015}$	Median intervals of boom and bust				
					T_{peak}	$T_{0.5}$	$T_{0.1}$	T_0	T_{b2b}
A. Fish reared in marine and brackish water									
Sustained	20	9.8	15.9	0.63^{a}	14.5^{a}				
Depleted	55	27.0	7.5	0.70^{a}	5^{ab}	3^{a}			
Collapsed	29	14.2	1.0	1.05^{b}	6^{ab}	1^{b}	5^{a}		13.0^{a}
Lost	100	49.0	1.3	1.50^{c}	5^{b}	2^{b}	4^{a}	5	10.5^{a}
All fish	204								
B. Molluscs									
Sustained	21	16	15.0	0.47^{a}	34^{a}				
Depleted	42	33	18.0	0.67^{a}	14^{a}	3^{a}			
Collapsed	24	19	1.3	0.95^{b}	10.5^{ab}	1.5^{b}	5.5^{a}		21^{a}
Lost	42	33	0.3	1.55^{c}	7^{b}	2^{ab}	4^{a}	6	13^{a}
All molluscs	129								
C. Crustaceans									
Sustained	8	7	9.2	0.53^{a}	5.5^{ab}				
Depleted	29	24	13.1	0.76^{a}	12^{b}	3^{a}			
Collapsed	25	21	7.2	1.16^{b}	7^{ab}	1^{ab}	5^{a}		18^{a}
Lost	58	48	1.0	1.38^{b}	5^{a}	2^{b}	4.5^{a}	5.5	11^{b}
All crustaceans	120								

Mean or median values sharing superscripts within a column of each section are statistically homogeneous.

distribution. For multiple comparisons, we used the Dwass, Steel, Critchlow-Fligner (DSCF) procedure to determine the significance of pairwise, two-sample rankings.

For each record, we calculated a coefficient of variation in production from the start of production to 2015 ($CV_{\text{Start-2015}}$), as a means of comparing variability in production across records. Note that this measure of temporal variation in production is independent of production status, a classification made strictly with reference to MAX, without regard to the axis of time. Statistical tests supporting differences among means or medians, as indicated by superscripts in Table 2, are in Appendix S1. Production records for the Pacific cupped oyster *Crassostrea gigas* (Table S1 in Appendix S1) illustrate how sparklines and the statistics described support the classification of status.

We used one-way ANOVA to compare CVs for different categories of production status, regression analysis to explore the association, by status, of maximum production and year of maximum production and logistic regression to relate the probability of loss of production to MAX, MXYR and T_{peak}, using SAS (SAS© 9.4; SAS Institute Inc., Cary, NC, USA). For logistic regression, we created a binary response variable, status (1, if production status is lost; 0, otherwise); the explanatory variables were MXYR, LOGMAX ($\log_{10}$-transformed maximum annual production), both continuous variables, a binary classification of T_{peak} (T_{p}CAT = 1, if $T_{\text{peak}} \leq 5$ years; 0, otherwise) and their interactions. Forward, backward and stepwise methods for selecting the optimum model produced the same result: status (event = '1') = MXYR + LOGMAX + T_{p}CAT + LOGMAX × T_{p}CAT. In this model, the probability, π, of status = 1, given a vector of explanatory variables, $\boldsymbol{x}$, is modelled as $\text{logit}(\pi) \equiv \log(\frac{\pi}{1-\pi}) = \alpha + \boldsymbol{\beta x}$; following analysis, the estimated probability, $\hat{\pi}$, can be calculated as, $\hat{\pi} = 1/(1 + e^{-\text{logit}(\hat{\pi})})$. We fit the model to records with MXYR ≤ 2010, allowing sufficient time for collapse (see Results), and then applied it to records with maximum production after 2010 but before 2015, to predict their probability of loss. Loss of production, by record, is then simulated by drawing a random number between zero and 1.0, assuming loss if the random number is less than or equal to the modelled probability of loss and summing the maximum production for all such simulated lost records; this simulation is repeated 100 times to estimate a mean and range of lost production.

Data availability

The data supporting the findings in this study are in the sources cited. Databases derived from primary sources are provided in Data S1–S3.

Results

Case studies

Aggregation of species in the FAO aquaculture production database (FAO 2017) creates an impression of stable or even increasing seafood supply, whereas underlying individual records show boom-and-bust production cycles. To illustrate this point, we present case studies of farmed marine molluscs and shrimp, which first brought this issue to our attention (detailed accounts in Appendix S1). The FAO record for Pacific oyster production in France, for example, confounds production of the Portuguese oyster and the Pacific oyster, thus obscuring the commercial extinction of the Portuguese oyster, because of a viral disease, in 1970–1973. Production of the Pacific oyster in France boomed in the 1980s, after large-scale introductions from Canada and Japan (Fig. 1a), peaked in 1996 at just below 150 000 t, but has declined to 75 100 t in recent years because of mass mortalities caused by ostreid herpes-like virus (Pernet *et al.* 2016). Aggregated and incomplete FAO records for production of abalones (*Haliotis* spp., Fig. 1b) and scallops (Pectinidae, Fig. 1c) in China obscure underlying records of boom-and-bust production. According to FAO data, abalone production began in China in 2003 and has increased since to 128 000 t in 2015. However, this record misses the boom-and-bust production cycles of Pacific abalone in northern China, which started in the mid-1980s and collapsed in the mid-2000s from bacterial disease (Table 1), and of small abalone in southern China, which started in the mid-1990s and collapsed by 2010 from bacterial and possibly viral disease (Table 1). A Chinese × Japanese Pacific abalone hybrid is currently the basis for abalone production in China (Zhang *et al.* 2004; Wu & Zhang 2016). Similarly, according to the FAO aggregated record for scallops in China, production began in 1979 (180 t) and increased to a peak of nearly 1.8 Mt in 2015. In reality, production of the zhikong scallop in northern China collapsed in the late 1990s from a viral disease; whereupon, repeated introductions of the non-native bay scallop fuelled a boom in production, which is now showing signs of potential collapse.

A notable feature of boom-and-bust production in our case studies is the sequential collapse of different species in a country or region. Production of the European flat oyster in France, which collapsed in 1982 after more than 100 years of cultivation, gave way to boom-and-bust production cycles for the Portuguese and Pacific oysters (Fig. 1a). Sequences of three species also occur in the cases of abalone in China (Fig. 1b) and shrimp in Thailand (Fig. 1e), while sequences of two species occur in the records of scallop production in China (Fig. 1c) and shrimp production in Taiwan (Fig. 1d). In these cases,

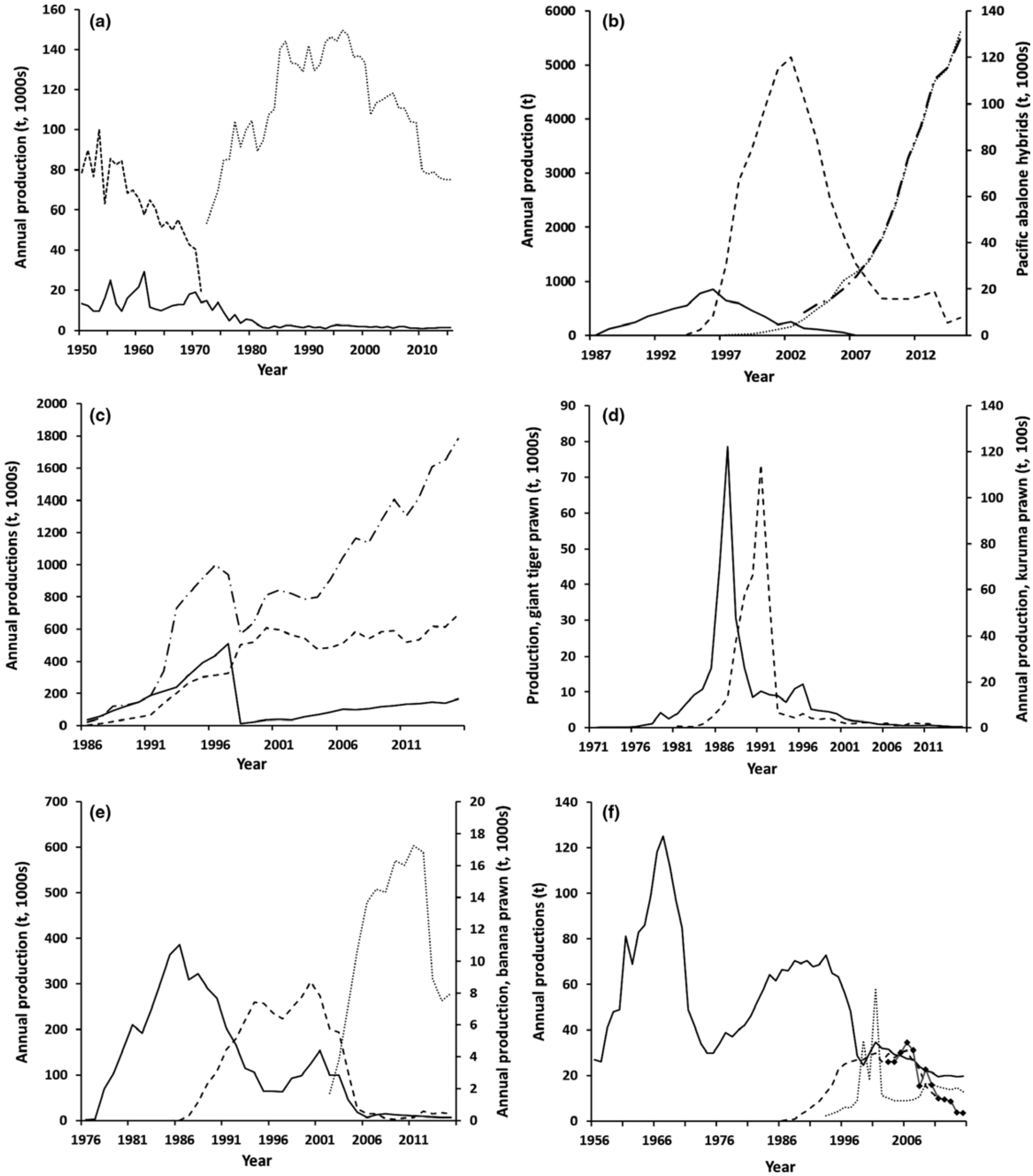

Figure 1 Boom-and-bust cases in molluscan and crustacean aquaculture. (a) Oyster production in France, *Ostrea edulis* (solid line), *Crassostrea angulata* (dash line), *Crassostrea gigas* (dot line). (——) European flat oyster; (-------) Portuguese oyster and (··········) Pacific cupped oyster; (b) production of Pacific abalone *Haliotis discus hannai* (solid line), small abalone *Haliotis diversicolor* (dash line) and Pacific abalone hybrids (dot line), in China, with FAO data for 'Abalone nei' (dot and dash line). (——) Pacific abalone; (-------) Small abalone; (··········) Pacific abalone hybrids and (— ·) FAO, Abalones nei; (c) production of zhikong scallop *Chlamys farreri* (solid line) and bay scallop *Argopectin irradians irradians* (dash line) in Shandong Province, China, with FAO data for 'Scallops nei'. (——) Zhikong Scallop; (- - -) Bay Scallop and (— ·) FAO, Scallops nei; (d) production of giant tiger prawn *Penaeus monodon* (solid line) and kuruma prawn *Penaeus japonicus* (dash line) in Taiwan. (——) Giant tiger prawn and (-------) Kuruma prawn; (e) production of banana prawn *Penaeus mergiensis* (solid line), giant tiger prawn *P. monodon* (dash line) and whiteleg shrimp *Penaeus vannamei* (dot line) in Thailand. (- - -) Giant tiger prawn; (··········) Whiteleg shrimp and (——) Banana prawn; and (f) Pearl oyster *Pinctada fucata* in Japan (solid line), China (dash line) and French Polynesia (dot line), with FAO data for China (solid line with diamond markers). (——) Pearl oysters, Japan; (-------) Pearl oysters, China; (··········) Pearl oysters, French Polynesia and (—◆—) FAO, China.

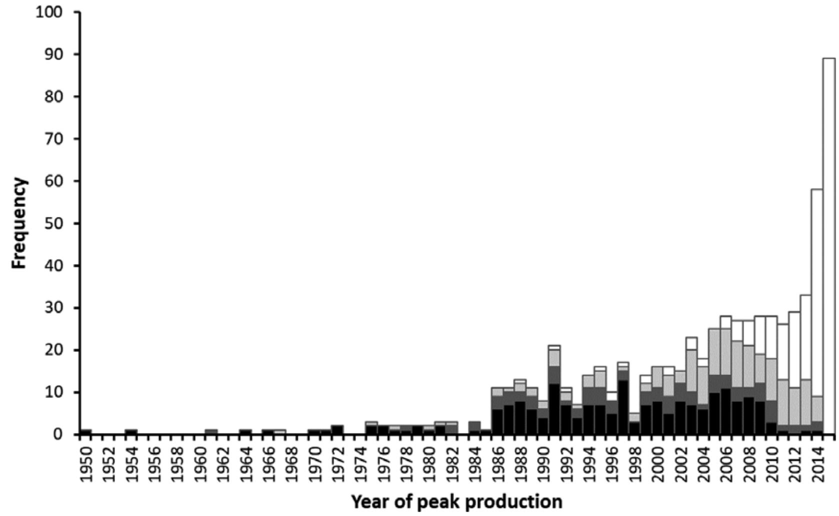

Figure 2 Distribution of years of maximum production. Frequency distribution of year of maximum production, by year, for FAO production records provisionally classified as sustained, depleted, collapsed and lost. Records for marine and brackish-water fishes, molluscs and crustaceans combined. (□) Sustained; (□) Depleted; (■) Collapsed and (■) Lost.

mostly caused by disease (Table 1; Appendix S1), farmers replace collapsed native species with new non-native species, to make up for loss of production, and the cycle repeats.

Finally, we include in our case studies, production of pearl oysters, because their economic worth far outweighs their small biological production. Despite an apparent economic incentive for sustaining production of pearl oysters, records in all six countries have a depleted status. In Indonesia, Papua New Guinea and Fiji, pearl oysters are commercially extinct. In China, French Polynesia and Japan, pearl oyster records show volatile production cycles, hovering just above collapse in 2015 (Fig. 1f).

Patterns in global production records

To determine how common boom-and-bust production cycles are on a global scale, we compiled and analysed the FAO's global database for farmed animal seafood production from 1950 to 2015 (FAO 2017). This database contains records of production, by country, for particular species or for species aggregated by genus or family. We provisionally classified the production status of each record into one of four, mutually exclusive categories – sustained, depleted, collapsed or lost – in relation to its peak or maximum production. Boom-and-bust production cycles are common across the three taxonomic groups. Records that fall provisionally into the collapsed or lost categories represent 40%, 37% and 50% of FAO records of fish, mollusc and crustacean production, respectively, even after exclusion of minor production records, which are predominantly collapsed or lost. However, the timing of peak production differs among the four categories of production status, with most 'sustained' records reaching peak production after 2010 (99 of 119 fish records (83.2%), 45 of 66 molluscan records (68.2%) and 45 of 53 crustacean records (84.9%), Fig. 2). These records of 'sustained' production account for the bulk of cumulative aquaculture production from 1950 to 2015 (344.2 of 526.0 Mt, 65.4%), but they have reached peak production too recently to show decline. Therefore, in order to characterize temporal features of different production-status categories, we restrict classification of records to those with peak production before 2011. This restriction captures almost all of the records provisionally classified as having lost or collapsed production, as well as records with longer histories of depleted or sustained production (Table 2).

Altogether, 278 of 453 (61.4%) records with peak productions before 2011 show collapsed or lost production. However, records of collapsed or lost production account for only 2.3%, 1.6% and 8.3% of cumulative production for fish, molluscs and crustaceans, respectively (Table 2). Sustained records of fish, molluscs and crustaceans, on the other hand, account for 15.9%, 15% and 9.2% of cumulative production, respectively, which suggests that larger records tend to have sustained production while smaller records are more likely to collapse or to be lost, a trend continued from the minor records, which we excluded. As expected, records with sustained or depleted production have half the variability in annual production as records with collapsed production and only about a third as much variability as records of lost production (Table 2, Average $CV_{Start\text{-}2015}$).

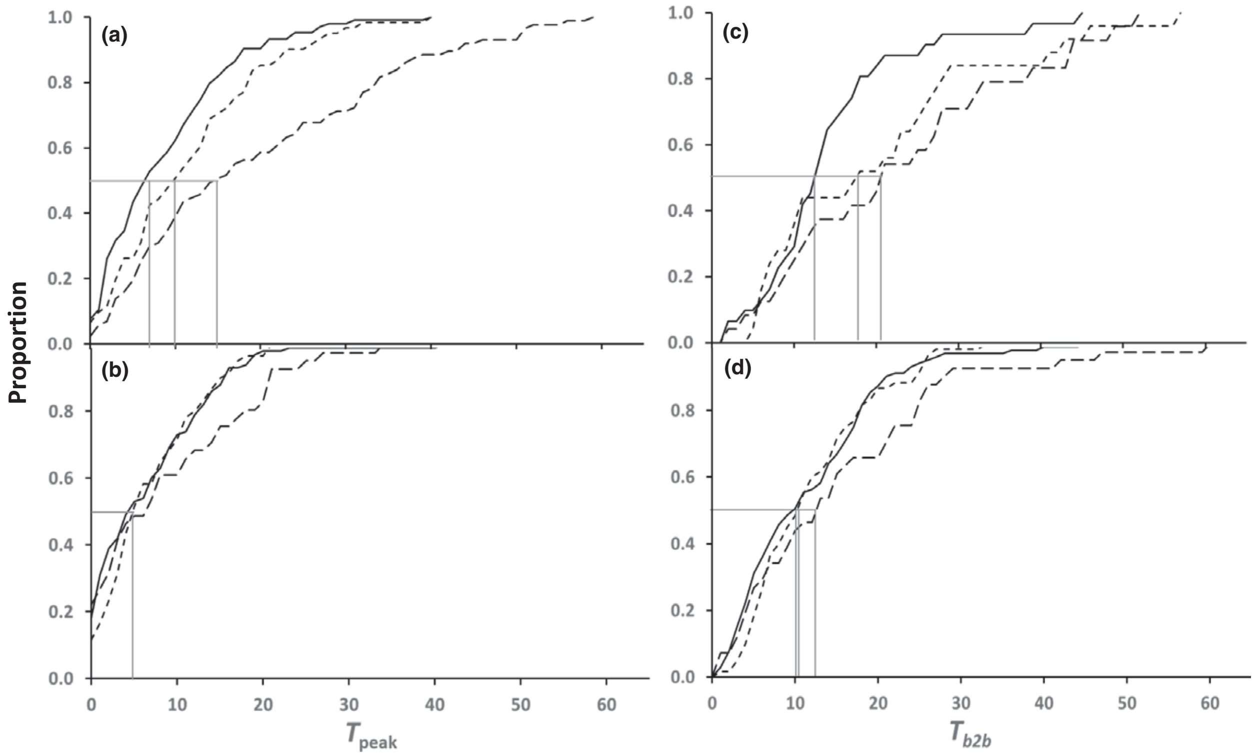

Figure 3 Distribution of boom times and boom-to-bust intervals. (a) Distributions of boom times (T_{peak}) for sustained, depleted and collapsed production records for marine and brackish-water fish (solid lines), molluscs (long-dashed lines) and crustaceans (short-dashed lines); medians of 7, 15 and 10 years, respectively, indicated by solid grey projections to the *x*-axis, are statistically heterogeneous. (b) Distributions of boom times (T_{peak}) in records of lost production for fish (solid lines), molluscs (long-dashed lines) and crustaceans (short-dashed lines); medians are statistically homogeneous, with a grand median of 5 years. (c) Distributions of boom-to-bust intervals (T_{b2b}) in records of collapsed production for fish (solid lines), molluscs (long-dashed lines) and crustaceans (short-dashed lines); medians are statistically homogeneous, with a grand median of 14 years. (d) Distributions of boom-to-bust intervals (T_{b2b}) in records of lost production for fish (solid lines), molluscs (long-dashed lines) and crustaceans (short-dashed lines); medians are statistically homogeneous, with a grand median of 11 years. See text and Table 2 for sample sizes and statistical tests.

Median lengths of the 'boom' phase, T_{peak}, for records of sustained, depleted or collapsed production – 7, 15 and 10 years, respectively – differ significantly among fish, molluscs and crustaceans ($\chi^2 = 26.1$, 2 d.f., $P < 0.0001$; Fig. 3a). This is attributable to the significantly longer median boom phase for molluscs ($P_{DSCF} \leq 0.0001$ for the comparison with fish, $P_{DSCF} = 0.0125$ for the comparison with crustaceans). In contrast, median boom phases for records of lost production in all three taxa are statistically homogeneous ($\chi^2 = 1.37$, 2 d.f., $P = 0.504$) and considerably shorter, with a grand median of only 5 years (Fig. 3b). T_{peak} is strongly associated with records of lost production: 103 of 181 records with $T_{peak} \leq 5$ years are lost (56.9%), while only 96 of 271 records with $T_{peak} > 5$ years are lost (35.4%); Fisher's exact $P = 8.15 \times 10^{-6}$.

Median lengths of the 'bust' phase, $T_{0.1}$, for records showing collapsed or lost production, are statistically homogeneous across the three taxa ($\chi^2 = 2.26$, 2 d.f., $P = 0.323$), with a grand median of 4 years. Median lengths of the boom-to-bust cycle, T_{b2b}, are likewise statistically homogeneous among records of collapsed production for all three taxa ($\chi^2 = 4.65$, 2 d.f., $P = 0.098$), with a grand median of 14 years (Fig. 3c). Medians for T_{b2b} are also homogeneous across records of lost production for fish, molluscs and crustaceans ($\chi^2 = 2.04$, 2 d.f., $P = 0.361$), with a grand median of only 11 years (Fig. 3d). The boom-to-bust cycle in seafood aquaculture has a decadal period, though with substantial variability.

Impact of boom-and-bust production on global aquaculture production of seafood

The historical accumulation of collapsed and lost records is associated with a slowing in the growth of annual production since 1996. The slowing in annual production is illustrated by deviation of observed global annual production from an exponential curve fit to the whole 66-year record

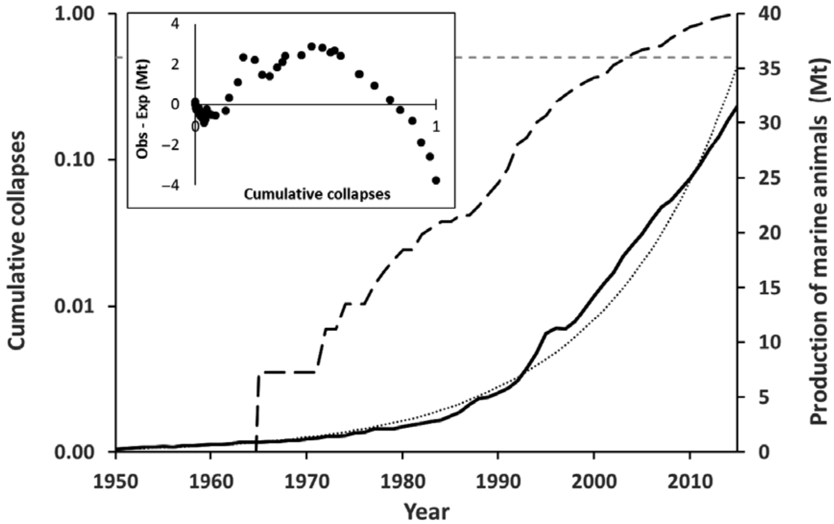

Figure 4 Relationship of boom-and-bust production to the recent slowing of animal aquaculture production. Cumulative distribution of year of collapse, on log scale (left vertical axis), from 1950 to 2015, for 287 records of collapsed or lost production for fish, molluscs and crustaceans combined (long-dashed line). Grey dashed horizontal line shows the median year of collapse, in 2004. Below, the annual production of seafood aquaculture (solid line, right vertical axis, in millions of metric tons), with fitted exponential line to highlight slow down in annual production since 1996. Inset shows relationship of cumulative collapses to the difference between the exponential fit and the observed production.

(Fig. 4; N.B., the purpose is not to fit a curve to the data but to highlight and index the recent slowing in growth). A plot of the deviation of production from this exponential curve versus the cumulative proportion of collapsed records (fish, molluscs and crustaceans combined; inset, Fig. 4), then, shows a significant negative trend in production, starting in 2004, when 52% of records had collapsed production. The deficit in 2015 amounts to slightly more than 3.75 Mt, which is equivalent to nearly 12% of that year's production and suggests that boom-and-bust production cycles may be associated with the slowing of growth in aquaculture production in recent years.

This association, however, appears at odds with the dominant contribution to cumulative animal seafood production of larger, sustained records (Table 2). The impact of boom-and-bust production is difficult to ascertain, because the recent expansion of aquaculture puts many extant records into the provisionally sustained category, necessarily diminishing the apparent contribution of collapsed records to cumulative production. Across all three taxa, averages of log-transformed maximum annual production for records provisionally classified as sustained, depleted, collapsed or lost are 3.97 (n = 238), 3.63 (n = 163), 3.34 (n = 84) and 2.91 (n = 203), respectively, reinforcing the notion that collapse and loss are primarily problems with smaller stocks. Nevertheless, the largest 30 collapsed or lost records have an average log maximum production of 4.4 (~25 000 t) and account for 2.37% (12.5 Mt) of cumulative seafood aquaculture production since 1950 (Table 2). Still, boom-and-bust production has decreased the cumulative production of farmed seafood by only a few per cent.

The impact of boom-and-bust production may be growing, however. Annual maxima for records of lost production have been increasing over the years (regression of log-transformed data, $F_{1,201} = 4.47$, $P = 0.031$; intercept, -14.551; slope, 0.00875), while those of provisionally sustained, depleted and collapsed stocks have been declining, though not at a rate significantly greater than zero (Fig. 5). At these rates, average peak production of records classified as lost would exceed those of records classified as collapsed, depleted and sustained by mid-century.

As noted (Fig. 2), many records have reached peak production too recently for collapse to occur, that is, after 2010, within the 4-year median time to collapse. Of these, 146 records reached peak production between 2011 and 2014 and more than 90% of these are classified provisionally as sustained or depleted (2015 is excluded, as the peak is undefined). We showed, above, that for records with a peak in production before 2011, a rapid boom in production (T_{peak} of 5 years or less) is a risk factor associated with a higher probability of lost production ($P = 0.569$). As year and size of maximum production also appeared to affect the probability of loss, we fit a logistic model relating the probability of loss of production to three explanatory variables, MXYR, LOGMAX and T_pCAT, and the interaction LOGMAX $\times$ T_pCAT, using records with MXYR $\leq$2010.

This model is highly significant (likelihood ratio $\chi^2 = 116.5$, 4 d.f., $P < 0.0001$), with a concordance index

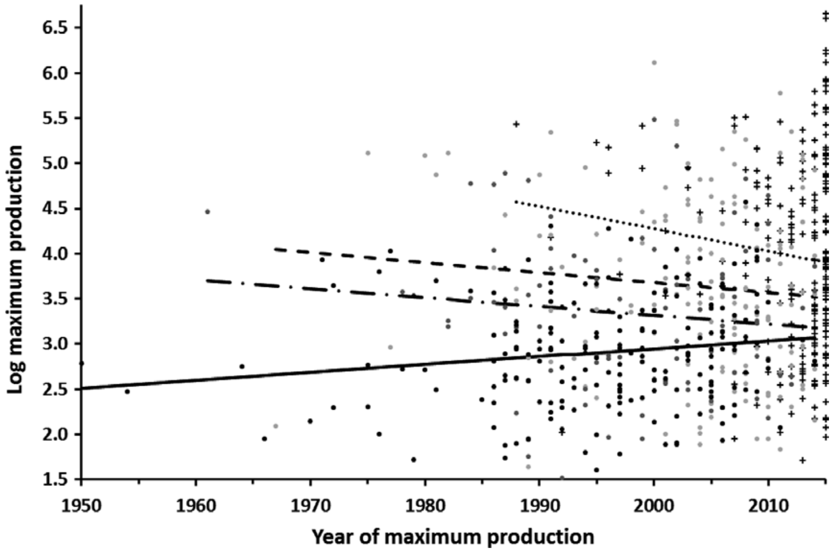

Figure 5 Maximum production by year of maximum production for four, provisional, production-status categories. Scatter plots of maximum production ($\log_{10}$), by year of maximum production, for farmed seafood production records provisional classified as 'sustained' (n = 238), depleted (n = 163), collapsed (n = 84) and lost (n = 203). Regression analysis revealed significantly heterogeneous slopes (status*year, P = 0.0038) among all four categories, but statistically homogeneous slopes for all records but those with lost production (status*year, P = 0.833). Regression lines for sustained, depleted and collapsed stocks from latter analysis; regression lines for lost-production records determined separately (slope = 0.00875, P = 0.031). (·········) 'Sustained'; (– –) Depleted; (— ·) Collapsed; (——) Lost; (+) S; (●) D; (●) C and (●) L.

of 0.775 for 50 347 pairs of responses. Response surfaces for the model (Fig. 6) confirm that the probability of loss decreases as annual maximum production (LOGMAX) and year of maximum production (MXYR) increase. Comparison of upper and lower panels in Figure 6 (a, without, and b, with the T_{peak} risk factor) illustrates how a rapid boom elevates the probability of loss, especially for records having moderately large and earlier peak annual production, the contribution of the interaction LOGMAX × T_{p}CAT.

Two-dimensional scatter plots (Fig. 7) illustrate how the explanatory variables affect the probability of loss for individual records. Among the 452 records used to estimate model parameters (small circles and squares), those that were actually lost (symbols with grey fill) tend to have higher probabilities of loss than those records not lost (open symbols). Records with short boom phases (squares) have higher probabilities of losses than records with long boom phases (circles), especially obvious in the plot against maximum production (Fig. 7b). Finally, predicted probabilities of loss for records peaking after 2010 are 1.5× to 5.5× times higher for records with short boom phases (filled triangles) than for records with long boom phases (open triangles), as log maximum production increases from 3 to 5 (Fig. 7b).

Using the parameters of the logistic regression model (Table 3), we estimate the probability of loss for each of the 143 extant records with peak production after 2010 (Fig. 7, triangles). Simulations based on these probabilities suggest that summed lost production from boom-and-bust production cycles would range from about 0.03 to 0.8 Mt (0.09% to 2.5% of 2015 animal seafood production, 31.6 Mt), with a mean of 0.22 Mt (0.7% of 2015 output).

The global boom in production of the whiteleg shrimp *Litopenaeus vannamei* offers a particularly striking example of the potential risk to animal seafood production. The 28 extant records of whiteleg shrimp production have a combined, cumulative production of 36 Mt, which represents a remarkable 40.6% of cumulative crustacean production since 1950 (88.6 Mt). Yet, the median year of peak production for these records is 2013. Based on estimated probabilities of loss, simulated annual lost production from boom-and-bust production cycles ranges from zero to 0.89 Mt, with a mean of 0.14 Mt, 0.45% of total 2015 animal seafood production but 3.6% of global whiteleg shrimp production in 2015.

Discussion

Our collection of case studies suggests that, despite a nearly exponential increase in global aquaculture production since 1950, prominent aquaculture species exhibit boom-and-bust production cycles on local, regional or national levels (Fig. 1). Several case studies of boom-and-bust production cycles are not evident in global data, owing to aggregation of production data over species or across regions. Moreover, most of the case studies show sequential boom-and-

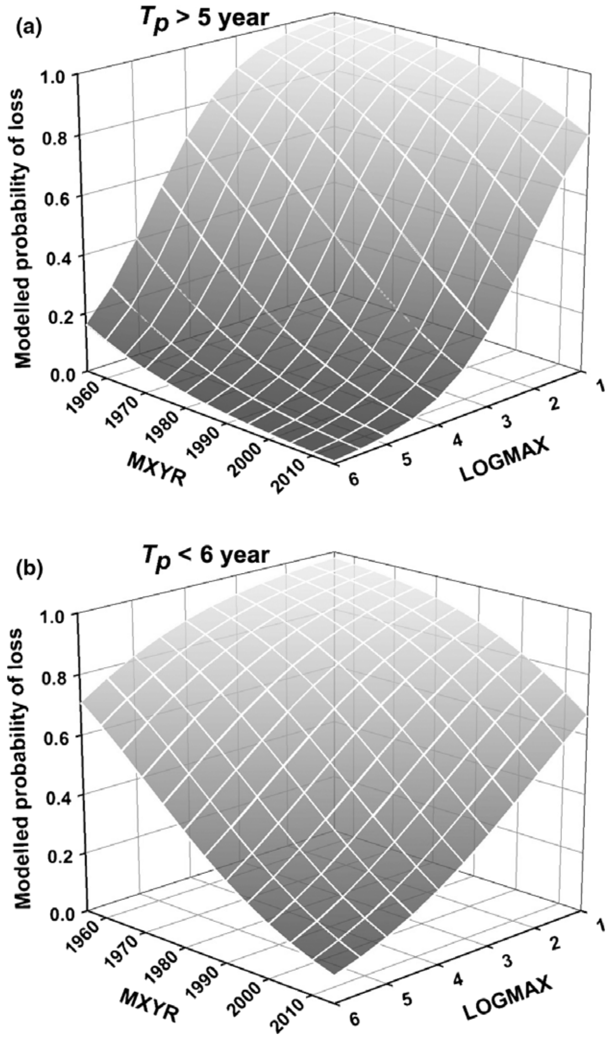

Figure 6 Surfaces showing the modelled response of the probability of lost production to the explanatory variables of maximum annual production and year of maximum annual production, without (a) and with (b) the risk factor of a rapid boom in production. Response is calculated from a logistical regression model (see text) of losses in FAO production records for molluscs and crustaceans and fish farmed in marine or brackish-water environments, which reached peaks in annual production prior to 2011. LOGMAX, $\log_{10}$-transformed maximum annual production in metric tons; MXYR, year of maximum annual production.

bust cycles within a country, which result largely from catastrophic diseases leading to the replacement of a native species with a non-native species (Table 1). How widespread such sequential collapses are is difficult to ascertain from global databases, but the concerns for global aquatic biodiversity raised by sequential collapses of aquaculture production are obvious. Species replacements via foreign introductions, for example Pacific oysters to France, bay scallops to China and whiteleg shrimp to Thailand, suggest that broodstock for artificial propagation of native species may no longer be available from depleted natural populations. Alternatively, the impact of farming on the local environment, perhaps, the establishment of a virulent disease, may have compromised the sustainability of natural populations. Recurrence of the boom–bust cycle, each time with a new species, suggests a domino effect on aquatic biodiversity that, if unchecked, could diminish marine and coastal biodiversity.

Our review of global data for the three main animal taxa contributing to farmed seafood production shows that boom-and-bust production cycles are common, particularly among the smaller production records (Table 2). Still, some large productions have been lost, the top 30 amounting to about 2.4% of cumulative seafood production since 1950 (Table 4). Several observations suggest that boom-and-bust production may have effects that are more substantial in the near future. First, the majority of cumulative seafood production comes from records reaching peak production between 2010 and 2014, too recently to have experienced a collapse (Fig. 2). Second, the slowing in the growth of aquaculture over the past 15 years correlates strongly with the increase in records of collapsed or lost production (Fig. 4). Third, the peak production of records that are ultimately lost is getting larger through time, while the peak production of records with sustained or depleted production is remaining the same or getting smaller through time (Fig. 5). Fourth, predicted probabilities of loss for stocks comprising the bulk of current production are nonzero and strongly associated with a rapid boom phase (Figs. 6,7); these probabilities translate into expected losses of a few per cent of total 2015 seafood production. Taken together, these observations suggest that boom-and-bust production cycles and their impact upon in seafood aquaculture bear scrutiny going forward.

Proximal causes of boom-and-bust production

Proximal causes of boom-and-bust production cycles are numerous and complex, including social, economic and ecological factors (e.g. Kautsky *et al.* 2000). The widespread involvement of disease (Table 1), especially in cases of sequential boom-and-bust cycles, suggests, however, that species replacements rarely reflect simple economic decisions by farmers based on markets. In France, a multidisciplinary investigation concluded that a complex interaction among various environmental, physiological and genetic factors, as well as pathogens, caused summer mortality of the Pacific oyster (Samain 2011). In Thailand, accumulation of organic waste and increased incidence of infectious diseases led to collapse of shrimp yields (Arquitt *et al.* 2005). In India, recurrence of disease, deterioration in water quality and marketing problems were the main factors responsible for collapse of farmed giant river prawn *Macrobrachium rosenbergii* (Nair & Salin 2012).

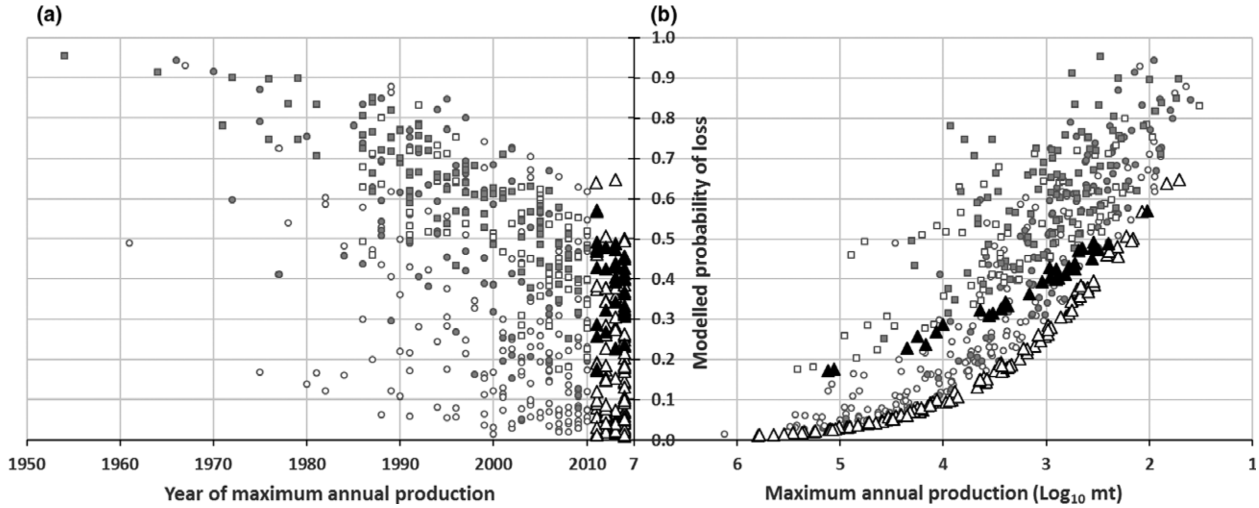

Figure 7 Scatter plots of probabilities of lost production for 599 records of animal seafood aquaculture, as a function of (a) year of maximum annual production. (○) T_{peak} > 5 years, extant; (●) T_{peak} > 5 years, lost; (□) $T_{peak} \leq 5$ years, extant; (■) $T_{peak} \leq 5$ years, lost; (△) T_{peak} > 5 years and (▲) $T_{peak} \leq 5$ years and (b) maximum annual production (log-transformed). Smaller circles and squares are records, which reached peak annual production prior to 2011 and whose losses were fit by a logistical regression model (see text). Circles are records without a boom, that is T_{peak} > 5 years; squares are records with a boom phase, that is $T_{peak} \leq 5$ years. Symbols filled with grey pattern are for records whose production was actually lost. Triangles are records, which reached peak production between 2011 and 2014 and whose probability of loss is predicted by the logistic regression model. Filled triangles are records with a boom phase; open triangles are records without a boom phase.

Table 3 Maximum likelihood estimates of intercept and slope parameters for a logistic regression model of the probability of lost production

Parameter	d.f.	Estimate	Standard error	Wald χ^2	Pr > χ^2
Intercept	1	110.5	24.1425	20.963	<.0001
MXYR	1	−0.0535	0.0121	19.7105	<.0001
LOGMAX	1	−1.2486	0.1887	43.7774	<.0001
T_pCAT	1	−1.3579	0.9664	1.9743	0.16
LOGMAX × T_pCAT	1	0.6469	0.2999	4.6528	0.031

Smallholder farmers, relying mainly on family labour, produce most of the world's aquaculture supply, on a vast geographic scale but with low efficiency. Africa and Asia, which together account for 90% of fish farmers, show average annual outputs of only 5.1 and 3.2 t per person per year, respectively (FAO 2016). In contrast, annual outputs in Europe, Oceania and North America average 28, 33 and 59 t per person, respectively, owing to a much higher degree of industrialization. The smallholder farming model appears to be closely associated with boom-and-bust production cycles. High returns to early adopters of a new species fuel rapid and uncontrolled proliferation of imitators, in numbers and densities far exceeding ecological carrying capacities (Arquitt *et al.* 2005). In addition, lack of organization among smallholders leads to excessive market competition among production zones during the bust phase. To reduce the risk of disease or the pressures of competition, smallholder farmers are quick to abandon aquatic farms or to shift to culturing other species, further accelerating local collapse.

A potential ultimate cause of boom-and-bust production cycles

A potential underlying ultimate cause of boom-and-bust production cycles in seafood production may be mismanagement of genetic resources. The hypothesis is simple: Loss of genetic diversity and increase in inbreeding, which can occur rapidly in highly fecund species with poor broodstock management or hatchery practices, result in a reduction in fitness, with heightened sensitivities to stress and disease, leading to mass mortalities and collapse (Doyle 2016). Systems models of boom-and-bust production (Arquitt *et al.* 2005; Prusty *et al.* 2014) have so far not accounted for the potentially nonlinear responses of production to intensification and ecological stress under inbreeding. We support the plausibility of this hypothesis with evidence concerning the population biology and genetics of marine fish and shellfish, which have a suite of life history traits – high fecundity, high early mortality and relatively long life (Winemiller & Rose 1992) – that make them susceptible to loss of genetic diversity and inbreeding.

Hatchery-propagated aquaculture stocks may have small effective population sizes for at least three reasons: (i) limited number of founders (founder effects, such as

Table 4 Top 30 FAO records with collapsed or lost production

Country	ASFIS common names	ASFIS species, genus names	MXYR	MAX	LOG MAX	Cumulative sum (t)
Iran (Islamic Rep. of)	Indian white prawn	*Penaeus indicus*	2004	8903	3.950	52 146
Vietnam	Metapenaeus shrimps nei	*Metapenaeus* spp	2009	9000	3.954	36 000
Vietnam	Indian white prawn	*Penaeus indicus*	2009	11 000	4.041	120 472
Ecuador	Blue shrimp	*Penaeus stylirostris*	1998	14 400	4.158	148 436
Saudi Arabia	Indian white prawn	*Penaeus indicus*	2009	21 051	4.323	144 880
Malaysia	Banana prawn	*Penaeus merguiensis*	2008	37 544	4.575	101 174
Philippines	Metapenaeus shrimps nei	*Metapenaeus* spp	1993	9490	3.977	42 084
India	Indian white prawn	*Penaeus indicus*	2008	10 600	4.025	122 032
Thailand	Banana prawn	*Penaeus merguiensis*	1986	11 031	4.043	138 251
Taiwan Province of China	Kuruma prawn	*Penaeus japonicus*	1991	11 469	4.060	42 020
Bangladesh	Penaeus shrimps nei	*Penaeus* spp	2008	67 197	4.827	1 105 973
Taiwan Province of China	Giant tiger prawn	*Penaeus monodon*	1987	78 548	4.895	329 168
China	Marine crabs nei	*Brachyura*	2002	156 166	5.194	862 735
Thailand	Giant tiger prawn	*Penaeus monodon*	2000	304 988	5.484	3 513 101
Faroe Islands	Rainbow trout	*Oncorhynchus mykiss*	2002	11 149	4.047	84 508
Indonesia	River eels nei	*Anguilla* spp	1996	18 839	4.275	42 259
Canada	Chinook (=King) salmon	*Oncorhynchus tshawytscha*	1991	20 147	4.304	152 687
Egypt	Grass carp (=White amur)	*Ctenopharyngodon idellus*	2003	88 277	4.946	540 437
Norway	Atlantic cod	*Gadus morhua*	2010	21 240	4.327	130 984
Japan	Coho (=Silver) salmon	*Oncorhynchus kisutch*	1991	25 730	4.410	428 910
Indonesia	Marine fishes nei	*Osteichthyes*	2010	43 690	4.640	110 210
Korea, Republic of	Japanese hard clam	*Meretrix lusoria*	1971	8521	3.930	60 002
Australia	Sydney cupped oyster	*Saccostrea commercialis*	1977	10 793	4.033	383 304
Malaysia	Green mussel	*Perna viridis*	2000	11 069	4.044	121 987
New Zealand	Pacific cupped oyster	*Crassostrea gigas*	1999	14 950	4.175	115 606
Korea, Republic of	Blood cockle	*Anadara granosa*	2007	28 372	4.453	468 219
France	European flat oyster	*Ostrea edulis*	1961	29 400	4.468	463 386
Korea, Republic of	Inflated ark	*Scapharca broughtonii*	1986	58 393	4.766	514 082
Germany	Blue mussel	*Mytilus edulis*	1984	59 311	4.773	990 880
Korea, Republic of	Japanese carpet shell	*Ruditapes philippinarum*	1989	64 973	4.813	1 090 461

the initial introduction of 26 bay scallops into China), (ii) high variance in the reproductive contributions of individual broodstock (Hedgecock & Pudovkin 2011; Table S2 in Appendix S1) and (iii) strong domestication selection (Sun *et al.* 2014; Gutierrez *et al.* 2016). Any or all of these factors may result in loss of genetic diversity and increases in inbreeding in hatchery-propagated aquaculture stocks.

Starting with Wilkins and Mathers (1973), many authors have compared genetic diversity in wild and cultured shellfish populations and concluded that hatchery-propagated populations lose genetic variation (Table S2 in Appendix S1, summarizes findings from 38 studies). Studies vary greatly with respect to the number of populations collected, the sample size for each population and the type and number of genetic markers used. Nevertheless, the evidence for substantial losses of genetic variation in cultured relative to wild populations is clear and consistent. The percentage reduction in numbers of alleles per locus in cultured versus wild records (45 individual comparisons) varies from 6.0% to 78.7%, with a mean of 34.3%; most reductions are between 20% and 50% (Table S2 in Appendix S1).

When estimated, effective population size (N_e) for cultured records ranges from 3.5 to 255, but most estimates are less than 50 (Table S2 in Appendix S1, n = 26). The median, N_e = 26.9, would allow an expected increase in inbreeding of 1.9% per generation. Despite a paucity of measurements, all studies report some degree of inbreeding depression (Evans *et al.* 2004; Keys *et al.* 2004; Moss *et al.* 2007; Gao *et al.* 2015). Marine species, especially oysters and other invertebrates, appear to have higher loads of deleterious mutations than terrestrial species (Launey & Hedgecock 2001; Plough & Hedgecock 2011; Plough 2016; Plough *et al.* 2016), so inbreeding depression is likely to be severe in these small hatchery-propagated populations. Comparative studies of quantitative-trait variation in wild and cultured aquaculture populations support this expectation (Wada 1986; Wada & Komaru 1994; Wilder *et al.* 1999; Zheng *et al.* 2004, 2008; Nair & Salin 2012).

Solutions

Solutions to proximal, ecological or biological causes of boom-and-bust production cycles, such as reducing intensification and exercising prudent biosecurity in the face of disease, are obvious and have been discussed elsewhere (e.g. Kautsky *et al.* 2000; Arquitt *et al.* 2005; Bondad-Reantaso *et al.* 2005; Prusty *et al.* 2014; Pernet *et al.* 2016). That rapid booms in seafood production are strongly associated with busts in production suggests that managing the rate of growth of seafood aquaculture on regional or national scales could reduce the probability of collapse.

If the ultimate cause of record collapse is mismanagement of genetic resources in highly fecund species, resulting in loss of genetic diversity, inbreeding and inbreeding depression, then the development of disciplined breeding programmes for major aquaculture species should be a management priority. Gjedrem *et al.* (2012) estimate that only 8.2% of aquaculture production in 2010 utilized records from family-based selection programmes, although Janssen *et al.* (2017) estimate that 80–83% of fish production in Europe now comes from selective breeding. Selective breeding programmes for salmon in Norway and tilapia in the Philippines and Malaysia provide notable examples of success, which need to be widely emulated. On the other hand, smallholders undertake their own programmes of artificial propagation rather than relying on disciplined breeding programmes, with the result that fragmented broodstock populations are too small to prevent loss of genetic diversity and inbreeding.

Finally, the sheer diversity of species in aquaculture may be another root cause of boom-and-bust production. Even after filtering for minimum production thresholds, the databases for marine or brackish-water fish, molluscs and crustaceans contain 95, 47 and 36 unique ‘species’, respectively, 178 taxa in all. This is undoubtedly an underestimate of the species diversity in seafood aquaculture, as some of these records aggregate data over genera or families. This number contrasts sharply with the handful of major terrestrial livestock species, cattle, goats, sheep, swine and several poultry. The knowledge base and research infrastructure in aquaculture are not sufficient to support the breeding and domestication of nearly 200 different species. Focus on a smaller number of major, global species would facilitate shared investments in the research and knowledge needed to breed high yielding, pathogen-free, disease- and stress-resistant records that are capable of adapting to a changing world and incapable of reproduction in the wild. Solving the ultimate causes of boom-and-bust production may require focusing resources on a much smaller number of species and investing in their chances of achieving sustainability through breeding.

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Supporting Information

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

Appendix S1. Additional narrative concerning case studies and detailed statistical analyses of global records.

Data S1. Mollusc time series.

Data S2. Crustacean time series.

Data S3. Teleost time series.