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Body size shifts and early warning signals precede the historic collapse of whale stocks

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Predicting population declines is a key challenge in the face of global environmental change. Abundance-based early warning signals have been shown to precede population collapses; however, such signals are sensitive to the low reliability of abundance estimates. Here, using historical data on whales harvested during the 20th century, we demonstrate that early warning signals can be present not only in the abundance data, but also in the more reliable body size data of wild populations. We show that during the period of commercial whaling, the mean body size of caught whales declined dramatically (by up to 4 m over a 70-year period), leading to early warning signals being detectable up to 40 years before the global collapse of whale stocks. Combining abundance and body size data can reduce the length of the time series required to predict collapse, and decrease the chances of false positive early warning signals.

Non-linear changes in the dynamics of complex ecological systems are often preceded by predictable changes in statistical properties of their time series[1,2]. Changes in metrics such as autocorrelation of an abundance time series form the basis of generic early warning signals theory, and suggest that regime shifts to alternative stable states, as well as population collapses that do not pass through catastrophic bifurcations, may be predicted well in advance of their occurrence[2–4]. However, although the theory underpinning this phenomenon is well understood[3,5], and such signals have been demonstrated in simulation and laboratory experiments[3,6], the possibility to detect and respond to early warning signals in real-world populations remains unclear[2,6,7]. This could be due to the reliability of such signals being highly dependent on the quality of the data analysed, with sampling protocols serving either to muffle or magnify statistical signals[6], or widely available proxies of abundance not necessarily reflecting underlying population dynamics[8]. These difficulties may be circumvented by analysing not only the time series of a population's abundance—as has been done classically[3]—but also the concurrent change in fitness-related phenotypic traits such as body size[9]. Ecological (that is, plastic) and evolutionary (that is, selection) responses to environmental perturbations can alter size distributions. Body size shifts affect population stability through changes in key demographic rates, including survival, growth and reproduction[10]. Consequently, changes in size distribution may affect the resilience of populations, potentially leading to regime shifts or population collapse[11]. In exploited systems, size-selective fishing has been shown to alter size distributions and increase variability in abundance due to reductions in the size structure of fish stocks[12], with the a priori expectation being that selective fishing decreases the variance of size distributions[13]. Thus, tracking shifts in body size alongside changes in the statistical properties of an abundance time series can provide two concurrent indicators of stability. While this potentially powerful approach has been demonstrated in experimental microcosms[9], it has yet to be evaluated for real-world collapses.

Although examples of overexploitation are widespread, few are as stark as the collapse of global whale stocks during the 20th century[14]. Commercial whaling flourished during the 1700s and 1800s as the slow-moving northern and southern right whale populations were harvested to the brink of extinction[15]. Technological advancements in the early 20th century opened up new whaling opportunities and the largely unchecked exploitation of global whale stocks[14,15]. While other exogenous factors—such as human-driven alterations to the food webs on which whales depend[16], or increasing pollution (both chemical[17] and aural[18])—cannot be exonerated from affecting the stability of whale populations, it is widely agreed that the main pressure exerted on this system was commercial whaling[15,19,20]. This overharvesting of whales led to the sequential collapse of populations as whalers moved from one species to another to maintain commercial viability[14]. The International Whaling Commission (IWC) has collated exceptional global records of 20th century commercial whaling, detailing the number of almost all and the size of most whales legally caught since 1900. These records provide the opportunity to test, for the first time, whether early warning signals are present before collapses of global whale stocks, and whether the inclusion of body size improves the reliability of any detected early warning signals[9].

Results

Population collapses and body size shifts. The collapse of whale fisheries followed a species-by-species sequence of discovery, exploitation and collapse, which can be observed in the numbers of each species caught over the 20th century[14]. It is generally accepted that fishing pressure remained high until whale populations collapsed and became commercially untenable, whereupon whale fisheries moved on to new species and the number of whales caught per year began to decline[14,15,19]. We show that the point at which the pressure exerted on whale populations began to decrease (identified by fitting generalized additive models (GAMs) to the global catch time series of four species, hereafter referred to as the 'inflection point') occurred well before the 1985 moratorium on commercial whaling (Fig. 1a; Supplementary Table 1). The only significant reduction in fishing effort prior to each infection point occurred during the period of World War II (1939–1945), after which commercial whaling continued at approximately pre-war levels (Fig. 1a).

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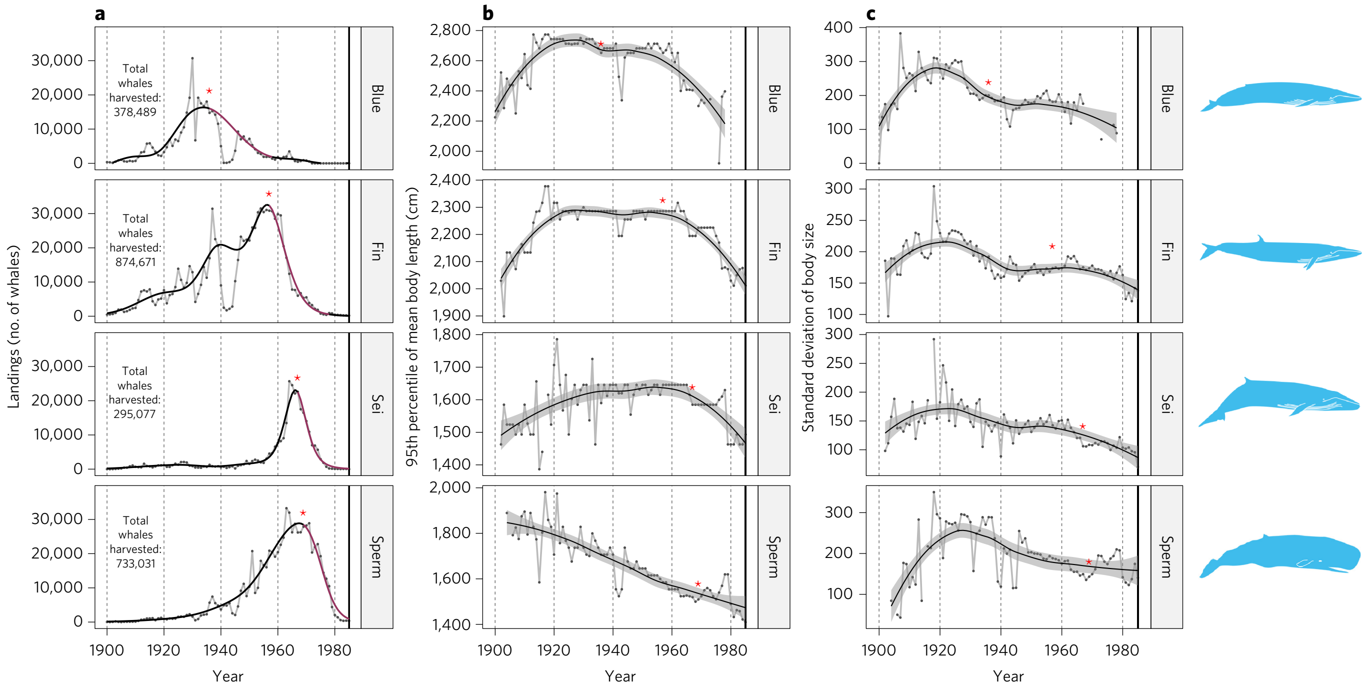

Figure 1 | Data from the IWC on the number and body size of whales caught from 1900 to 1985. a–c, Time series of number of whales caught per year (**a**), 95th percentile of body size (**b**), and standard deviation of body size calculated from records of individual whales caught between 1900 and 1985 (**c**) (the year of the moratorium on commercial whaling, vertical black lines). Pressure on a population was inferred to have declined when the number of individuals of a species caught per year declined significantly (*$P < 0.05$), quantified by fitting GAMs to the landings data (GAM fits plotted on top of landings data, red segments indicate periods of significant decline). Locally weighted scatterplot smoothing (LOESS) indicates trends in body size data over time and grey shading indicates the 95% confidence intervals for the smoothing. Whale illustrations: K. Askaroff.

During this period of commercial whaling, there were substantial shifts in the size distribution of whales caught (Fig. 1b). For blue (*Balaenoptera musculus*), fin (*B. physalus*) and sei (*B. borealis*) whales, the 95th percentile body size showed increases in the first half of the 20th century (3 m for blue whales, 2 m for fin and 1 m for sei), followed by gradual declines (Fig. 1b). These increases in body size may be an artefact of fishing technological advancement, which peaked in 1930[21], or may reflect the harvesting of individuals from different locations (Supplementary Fig. 5). Subsequent declines in body size probably reflect a true shift in the body size distribution of the populations, through the direct removal and scarcity of large individuals, as reported for many fish populations that have undergone size-selective fishing pressure[22]. Conversely, sperm whale (*Physeter macrocephalus*) sizes declined continuously, with individuals caught in the 1980s measuring on average 4 m shorter than those caught in 1905 (Fig. 1b). This alternate body size shift in sperm whales may be due to their lower maximum speed, minimizing the artefact of technological advancement[23]. The standard deviation of body size, a descriptor of the size diversity and stability of a population[12], showed a consistent pattern across the four species; increases in the standard deviation occurred over the initial years of fishing and technological advancement, followed by declines as the largest individuals were selectively removed (Fig. 1c). Shifts in mean body size prior to the identified inflection points were small for all species bar the sperm whale; however, all four species showed characteristic increases and subsequent decreases in the standard deviation of body size (Fig. 1b,c).

Detecting early warning signals. The IWC data set provides an ideal opportunity to test the applicability of trait-inclusive early warning metrics, as it contains data on the size dynamics and catches—the number of whales caught per year—for populations known to collapse. These data were analysed using the framework proposed in ref. [9], where an early warning signal is a binary response—present or not—for a given time series. Early warning signals were present for all four species when the full time series were analysed (Fig. 2). Size-only metrics generated early warning signals for two of the four species, whereas catch-only metrics produced early warning signals for

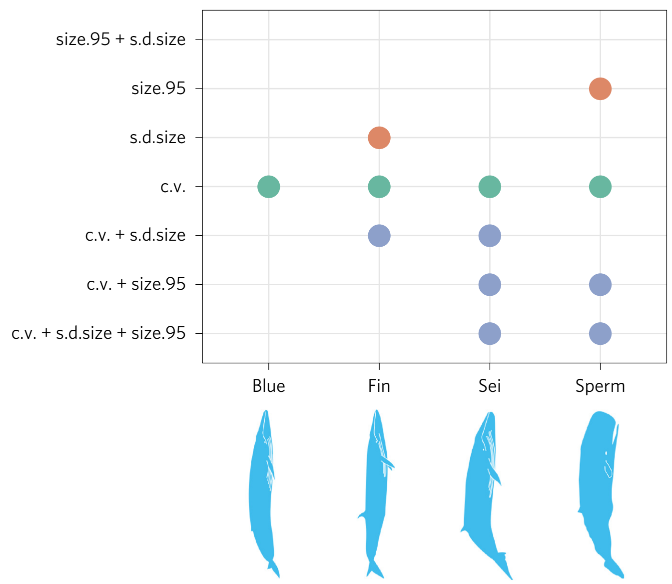

Figure 2 | Metrics that include body-size-only (orange), catch-only (green) and size–catch (blue) data, which produced early warning signals in each population prior to the inflection point of the fishery. Data from the first recorded landing after 1900 until the year before the inflection point were analysed. Whale illustrations: K. Askaroff.

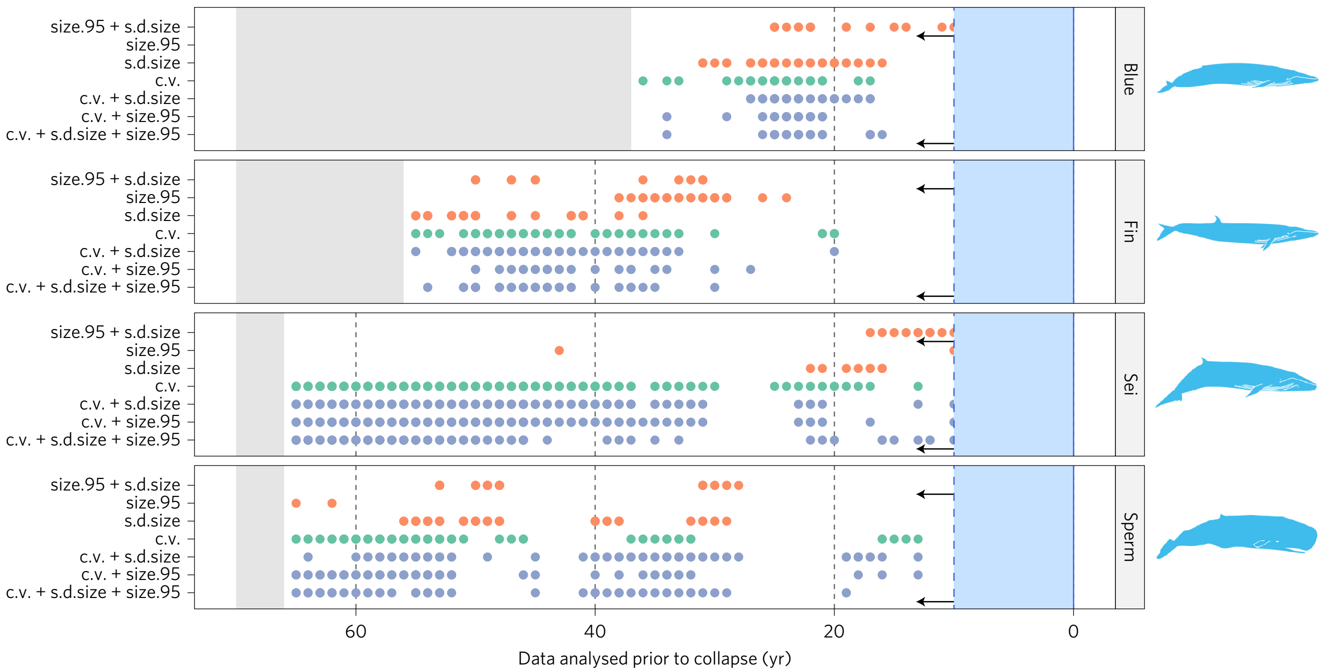

Figure 3 | Early warning signals were detectable with as little as 10 years of data prior to the inflection point. Increasing the window size typically increased the prevalence of early warning signals. Points show an early warning signal present using size-only data (orange), catch-only data (green), or size–catch data (blue). Blue shaded areas indicate the 10-year starting window. Arrows show the increasing size of the window analysed. Grey shaded areas indicate no further data are present. Whale illustrations: K. Askaroff.

all four of the species. The metrics that included both body size and catch data—a combination proposed to be least susceptible to false identification of early warning signals[9]—produced signals in three of the four species (Fig. 2).

The presence of early warnings signals in a given time series, although important, does not address two critical questions for management: (1) what are the minimum data required to predict a collapse? (2) How long before a collapse are early warning signals present? The minimum data required to generate early warning signals can be investigated by analysing data directly before each inflection point (Fig. 1a), where the pressure on the system—and consequently its instability—is theoretically highest, and thus early warning signals would be expected to be most detectable. Moving backwards using an expanding window bound 1 year before the inflection point in catch data, and iteratively adding data points, we show that all species display early warning signals prior to inflection points when 20 years or less of data were analysed (Fig. 3). Metrics that incorporated size data required the same amount or, in the case of blue and sei whales, less data than catch-only metrics (Figs 1 and 3).

To be useful, early warning methods must also be able to reliably predict collapses far enough in advance to make intervention possible[24]. One major problem to overcome is the low signal-to-noise ratio associated with high-dimensional systems such as those found in ecology, which may generate erroneous early warning signals[6]. We cannot account specifically for false positive signals in this analysis (all populations are under intense fishing pressure and data on control populations are unavailable). However, as a tipping point is approached—and thus a system's resilience declines—statistical signals embedded in the analysed time series data are predicted to become more detectable[5]. Early warning signals present in multiple consecutive or near-consecutive time steps, indicating increased instability of the system, are therefore more likely to reflect true positive signals. Conversely, isolated signals may reflect vagaries in the data, and thus are more likely to be false positives. Using a 20-year rolling window (the maximum length required to generate an early warning signal), we show that consecutive early warning signals were generated far in advance the inflection point of each species by multiple metrics (Fig. 4). In the case of the sperm whale, these consecutive signals were present up to 40 years, or approximately four generations[25], before the decline in size-catch and catch-only metrics, and 30 years before the decline in size-only metrics. Size-catch metrics performed similarly to those that were based on catch-only data, whereas size-only metrics generated consecutive early warning signals later than either size-catch or catch-only metrics.

Discussion

Ecosystems are being subjected to ever increasing human pressures, with consequences ranging from the extinction or extirpation of species, to large-scale regime shifts and associated loss of ecosystem services[26]. We show for the first time that early warning signals of an impending population collapse are independently detectable in both the trait and catch data from real-world population declines, as well as being generated by metrics that combine these two data types. The IWC data set provides an excellent opportunity to detect early warning signals, as it collates data on every legally caught whale over an 85-year period[15]. This high data quality may explain the relatively good performance of our catch-only metrics. However, the veracity of catch data reflecting underlying population dynamics remains uncertain[8], and as such it is important to recognize the potential limitations of using such data to search for early warning signals. Furthermore, abundance-based early warning signals are susceptible to the influence of exogenous factors such as spatial subsampling[6,8], or, in the example data given here, year-to-year fluctuations in whaling effort driven by technological advancement or the number of ships/countries involved in whaling. Conversely, because size-based early warning signals take the mean of multiple individuals (rather than the sum of individuals caught), they are likely to be significantly more robust to sampling protocols[9]. We demonstrate that size-catch and size-only early warning signals are present prior to real-world population collapses. Size-based metrics are less susceptible to the data quality issues identified above, and composite size-catch metrics require concurrent changes in two

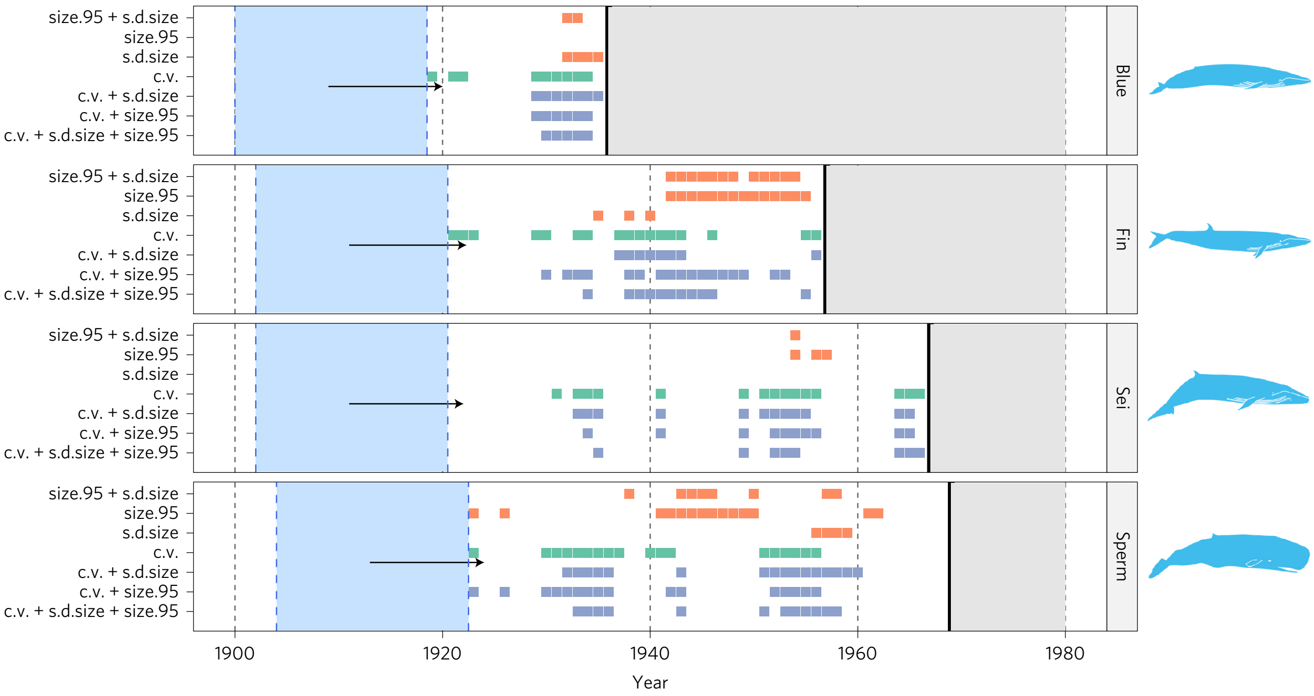

Figure 4 | Consistent early warning signals were present up to 40 years prior to inflection points. Metrics that included size tended to produce consistent early warning signals approximately concurrent with those metrics based on catch-only data. Black vertical lines show the inflection point for each species, blue shaded areas indicate the 20-year rolling window used to calculate early warning signals and points indicate the presence of an early warning signal using size-only data (orange), catch-only data (green), or size–catch data (blue). Whale illustrations: K. Askaroff.

measures of stability (size and abundance) to generate a signal[6,9], suggesting that the inclusion of body size dynamics will provide greater confidence in the detection of collapse than catch-only early warning signals. Indeed, trait dynamics shifts may be used to predict collapse in the absence of reliable catch data—for example, in relation to practices such as shark finning, where catch records are incomplete[27]—but size distributions may be inferred from the fins themselves. The authors envisage the application of early warning signals to such data as a simple-to-implement, first-pass analysis to identify populations at risk of collapse, and note that (as with any other predictive method) they will be susceptible to false positive or negative results. However, such a first-pass analysis would allow further, targeted, in-depth investigation to assess more thoroughly the likelihood of the predicted collapse, and under what circumstances it would occur.

Methods

Whaling data. Data on historical whaling were provided by the IWC (www.iwc.int) and are open access. The data set comprises records of every known whale caught by commercial whaling forays conducted from 1900 onwards (with the exception of whaling carried out by the USSR in the Southern Hemisphere (C. Allison, IWC, personal communication)). For a subset of these whales, there are records of the length of individuals caught. These data contain catch information for 15 different species of whale (Supplementary Fig. 1). Of these, we selected four species to analyse based on the following criteria: (1) excluding any species known to have already exhibited a population crash prior to 1900 (right whale); (2) excluding any species where the observed decline in the number of individuals caught was confounded by the introduction of the moratorium on commercial whaling (Brydes whale, pilot whale); (3) excluding any species that did not show a significant decline in landings (killer whale); (4) excluding any species where there was a significant proportion of the time series where no body size data were available (gray whale); and (5) excluding any species that did not show a clear inflection point (for example, had multiple peaks in harvesting effort, or only declines in harvesting) (humpback whale, bowhead whale) (Supplementary Fig. 1). The number of individuals caught per year, the 95th percentile of body size, mean body size and the standard deviation of body size were then calculated from records of individuals caught for the blue, fin, sperm and sei whales.

Historically, there have been size limitations on the minimum length of species that can be legally taken, and for some species (such as the sperm whale) the maximum size that can be legally taken during certain months of the year[28]. These restrictions may have truncated the size distribution of caught individuals, especially across the smaller size classes. Therefore, to gain a robust indication of how body size of the populations may have changed through time, we calculated the 95th percentile of body size, as this would be less affected by fishing practices, although the trends and results generated using mean body size are similar (see below)[29].

Identifying inflection points. We identify the time point at which pressures on the system began to decline using the method proposed in ref. [7], whereby GAMs were fitted to the landings time series using the mgcv package[30] in the statistical environment R[31]. The number of spline knots was automatically selected using generalized cross-validation[30]. The points in time at which the fitted spline declined significantly were then calculated from the first derivative of the fitted spline with respect to time, calculated using finite differences, as well as 95% pointwise confidence intervals to assess whether the gradient was significantly different from zero. The inflection point of the population was then defined as the first year of significant decline (Fig. 1; Supplementary Table 1). The inflection point therefore defines when the pressures exerted on the system were greatest, and thus the time up to which early warning signals should be regularly present. Analysis of early warning signals was thus run on data up to the year before the inflection point. Given the generation times of these organisms (~18–27 years[32]), these pre-inflection-point time series represent around 1.8–3.8 generations of the species tested. To our knowledge, no work has yet been done on the effects of time series length relative to generation time on the presences of early warning signals; however, our results seem to show that these time series may be long enough to make such signals detectable, although further effort should be invested in ascertaining what time scales are sensible across which to calculate early warning signals.

Calculation of early warning signals. The presence of early warning signals was calculated using the framework developed in ref. [9], based on that of ref. [3]. This framework allows either single or multiple leading indicators of population collapse to be combined to produce a single composite metric of risk[9].

Previous work has suggested that the most robust method to predict population collapse is a composite metric composed of the coefficient of variation (c.v.), change in mean size (mean.size) and the change in the standard deviation of size (s.d.size): c.v. + mean.size + s.d.size (ref. [9]). Although this experimental system is unlikely to reflect all real-world population collapses, it is nonetheless informative to see whether the best predictor of collapse in such a small-scale system can predict large scale real-world collapses. Of these three leading indicators, c.v. and s.d.size were predicted to increase before a collapse, whereas mean.size was predicted to decrease[5,9]. Work in fisheries has suggested that the 95th percentile of body size provides a more robust measure of shifts in body size than mean body size[29], thus here we include the 95th percentile of body size in the main text as a conservative analysis, and present the results of the same analyses run with mean body size in Supplementary Note 1. Previous work showed that the standard deviation of size will increase before a collapse that is driven by deteriorating environmental conditions[9,33]. However, in harvested systems such as fisheries, this is unlikely to be the case as large individuals are selectively removed from the population, leading to shifts to smaller bodied individuals and consequently decreases in the standard deviation of body size, potentially leading to increasing instability[12]. Thus, here we consider significant declines in the standard deviation of body size to be a warning signal of decreased stability of a population.

To test the efficacy of this composite metric, and the relative importance of the terms included within it, we tested a range of early warning metrics composed of different combinations of the leading indicators c.v., mean.size and s.d.size (Fig. 2).

As in ref. [9], each of these three leading indicators (c.v., 95th percentile body size (size.95) and s.d.size) was calculated for each species' time series independently, and at each year. Each leading indicator was then normalized by subtracting the long-run average of that indicator from the value of that indicator at time t, and dividing by the long-run standard deviation. Thus, each statistic at time $t(\hat{w}_t)$ was calculated as:

$$\hat{w}_t = \frac{w_t - \overline{w}_{1:t}}{sd(w_{1:t})}$$

where $w_{1:t}$ is the mean of a statistic from times 1 to t, and s.d.$(w_{1:t})$ is the standard deviation over the same period. Composite metrics were then calculated by summing the values for the leading indicators to be included at each time point. An early warning signal is then considered to be present when the value of the composite metric at any point exceeds its running mean value by more than 2 σ.

Simply, this method quantifies how a composite metric changes relative to the start of the time series analysed. Ideally, the data from the beginning of the time series should thus come from a period where the pressures exerted on the system are low (and therefore the system is stable), which is the case in the whaling data (Fig. 1a, 1900–1910). The composite metric approach then quantifies whether there is a significant increase (trend) in the composite index as the pressure on the system increases (Fig. 1a, 1910 onwards), relative to this period where the pressures on the system are low. Use of a rolling mean ensures that the change in the system through time must be significantly rapid relative to background fluctuations for a 2 σ threshold to be crossed, and thus an early warning signal to be generated, giving a clear presence/absence response on which conservation decision-making can be based.

As body size and, in harvested systems, the standard deviation of body size are expected to decrease as a collapse is approached[9], the normalized leading indicator values for body size and standard deviation of body size were multiplied by −1 to allow it to be included within the composite metrics. Thus, a composite index composed of c.v., mean body size and the standard deviation of body size incorporates three different measures of stability—two based on trait dynamics, and one on abundance dynamics.

Analysis of early warning signals. We analysed the presence of early warning signals in three different ways. The first is an analysis of the entire time series for each whale species from the first recorded landing after 1900 until the year before the decline in landings. This approach gives a general idea of how predictable the collapse was when analysing all the available data (Fig. 2).

As the quality of the data used to generate early warning signals is known to significantly affect our ability to correctly identify whether a population is at risk of collapse, and in a management scenario one would want to predict a decline as far in advance as possible, we performed two further analyses where the amount of data used to calculate early warning signals was manipulated.

The second approach calculated the minimum length of the time series required to generate an early warning signal, a key issue for conservation decision-making (Fig. 3). We did this by analysing the 10 years of data directly prior to the inflection point in landings observed in each species (Supplementary Table 1). We calculated whether an early warning signal was present, and then iteratively added additional years to the analysis. As this approach was bound by the decline in landings, any early warning signals generated could be considered true positive results. This approach indicated how sensitive our results were to varying window size, and whether including trait-based methods required more or less data to generate a true positive signal (Fig. 3).

The third approach investigated the predictive accuracy, and consistency, of the early warning metrics tested. To make predictions about future collapses, it is essential to know how robust the methods are to the vagaries of the data available; however, without control populations that do not collapse[2,3], determining whether a signal is a true positive or false positive can be problematic. Previous work has suggested that an arbitrary time frame (say, 10 years into the future) could be used to assess whether an early warning signal is a true positive or not, with a true positive being recorded if there are significant declines in the population during that 10-year window [7]. However, this approach is problematic, as the life history of the species is likely to significantly affect the time frame over which one should search for significant declines. To circumvent this issue, we analyse the data on whale landings using a 20-year rolling window approach (Fig. 4). Twenty years was selected as a window length as it is the maximum length required to generate an early warning signal using the final years before an inflection point (Fig. 3), and is also the length of data used for previous work that included trait-based early warning indicators[9]. This was implemented by analysing the first 20 years of each time series (from 1900 onwards) for an early warning signal, recording whether a signal was present, and then moving the 20-year window of analysis forward by 1 year and re-analysing the data. As a tipping point is approached, the system will, theoretically, become less and less stable, so early warning signals should continue to be present in the analysed data[5]. Thus, we considered early warning signals that are generated from a 20-year window of the time series of a species to be reliable if they were followed by recurring early warning signals as an inflection point (the point of maximum instability in the system) was approached (Fig. 4). Isolated occurrences of early warning signals were considered less reliable.

We present the above analyses on two different data sets. The first (that presented in the main text) is an analysis of the global data on whale catches. In addition to this global analysis, and to test for effects of different spatial scales, we performed a secondary analysis on data from only Southern Hemisphere whaling catches (Supplementary Note 2). The Southern Hemisphere is a region previously used for the assessment of whaling on whale stocks, and where the majority of whales were caught in the IWC data[14].

Data availability. Data are freely available on request from the International Whaling Commission (https://iwc.int/).

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Author contributions
This work was jointly conceived by all the authors. C.F.C. performed the analyses and wrote the first draft of the manuscript. All co-authors contributed substantially to revisions.

Additional information
Supplementary information is available for this paper.

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Competing interests
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