Population dynamics of marine fishes at low abundance

David M. Keith and Jeffrey A. Hutchings

Abstract: The recovery of depleted species depends on their population dynamics at low abundance. Classical population growth models, applied widely in fisheries science, assume that per capita offspring production increases as abundance declines (compensation). However, slow or absent recovery by many depleted fishes might reflect unexpectedly weak compensation or the presence of Allee effects (depensation). Using meta-analytical techniques to describe reproductive dynamics, we find considerable variability among 207 exploited marine fish stocks (104 species) in how standardized per capita population growth changes with abundance. Although many species exhibit strong compensatory dynamics (negative density dependence), others show much weaker compensation than expected, and some exhibit evidence of an Allee effect, such as Atlantic cod (*Gadus morhua*) and Alaskan walleye pollock (*Theragra chalcogramma*). As data at low levels of abundance become increasingly available, it appears that compensation, while strong in some species, is comparatively weak or nonexistent in others, thus providing an explanation for why the recovery of some depleted stocks, despite reductions in exploitation, has been considerably less than what classic models of population growth would otherwise suggest.

Résumé : Le rétablissement d'espèces en déclin dépend de la dynamique de leurs populations à faible abondance. Les modèles de croissance des populations classiques, couramment appliqués en sciences halieutiques, partent du principe que la production de descendants par tête augmente quand l'abondance diminue (compensation). Toutefois, le rétablissement lent ou nul de nombreuses espèces de poissons en déclin pourrait refléter une plus faible compensation que prévu ou la présence d'effets Allee (dépensation). À l'aide de techniques méta-analytiques utilisées pour décrire la dynamique de reproduction, nous avons relevé une variabilité considérable parmi 207 stocks de poissons marins exploités (104 espèces) pour ce qui est de l'évolution de la croissance normalisée de la population par tête en fonction de l'abondance. Bien que de nombreuses espèces présentent une forte dynamique compensatoire (dépendance négative de la densité), chez d'autres espèces, la compensation est beaucoup plus faible que prévu, et certaines, comme la morue (*Gadus morhua*) et la goberge de l'Alaska (*Theragra chalcogramma*), montrent des signes de la présence d'un effet Allee. À la lumière d'un ensemble croissant de données à faibles niveaux d'abondance, il semble que la compensation, bien que prononcée pour certaines espèces, soit comparativement faible ou non existante pour d'autres espèces, ce qui expliquerait pourquoi, malgré une diminution de leur exploitation, certains stocks en déclin présentent un rétablissement beaucoup moins important que ce que les modèles classiques de croissance des populations porteraient par ailleurs à croire.

[Traduit par la Rédaction]

Introduction

Numerous marine fishes have experienced unprecedented fishing-induced declines over the last half-century (Hutchings et al. 2010). Despite considerable reductions in fishing mortality (Worm et al. 2009), many stocks have not recovered at the rate that would have been predicted based on classical and stationary population dynamics (Hutchings 2001; de Séligny et al. 2010; Hutchings and Rangeley 2011).

Historically, studies of the population dynamics of commercially exploited fishes, including numerical responses to changes in fishing mortality, have relied on Ricker and Beverton–Holt stock–recruitment (S–R) models to describe the relationship between abundance and offspring production (Ricker 1954, 1958; Beverton and Holt 1957). Both of these formulations predict that per capita recruitment (recruitment is the number of offspring that survive to enter a fishery) will increase as abundance declines. The compensatory (negative density-dependent) relationship between per capita recruitment and abundance has underlain much of fisheries management, although even Ricker acknowledged the limitations of his model, remarking that "poor resistance to exploitation at low stock densities" (Ricker 1958, p. 999) was evident in some Pacific salmon (*Oncorhynchus* spp.) populations. More recently, the use of these models has been questioned because of the observation that nonparametric models can provide more robust alternatives to the fitting of an S–R relationship when the actual relationship is unknown (Munch et al. 2005). Despite these caveats, there has been little effort

Received 24 August 2011. Accepted 24 April 2012. Published at www.nrcresearchpress.com/cjfas on 29 June 2012.
J2011-0355

Paper handled by Associate Editor Ray Hilborn.

D.M. Keith. Department of Biology, Life Science Centre, Dalhousie University, 1459 Oxford Street, Halifax, NS B3H 4R2, Canada.
J.A. Hutchings. Department of Biology, Life Science Centre, Dalhousie University, 1459 Oxford Street, Halifax, NS B3H 4R2, Canada; Centre for Ecological and Evolutionary Synthesis, Department of Biology, University of Oslo, NO-0316 Oslo, Norway.

Corresponding author: David M. Keith (e-mail: keithdm@dal.ca).

to account for a lack of strong compensation at low abundance, in part because of an absence of strong empirical support for the existence of Allee effects, or depensation, in meta-analyses of marine fishes (Myers et al. 1995; Liermann and Hilborn 1997). Slow or absent recovery in many depleted populations (Hutchings 2000), despite reductions in fishing mortality (Hutchings 2001), has led to suggestions that Allee effects might comprise a more important component of marine fish population dynamics than previously thought (Shelton and Healey 1999; Frank and Brickman 2000; Hutchings and Reynolds 2004).

Thus, the question of whether per capita recruitment generally increases with declining abundance when populations are at very low abundance is a fundamentally important one from a conservation and resource management perspective. Although previous research has generally failed to detect an Allee effect in marine fishes, the statistical power of these analyses was comparatively low, primarily because of the paucity of recruitment data available at low levels of spawning stock abundance (Myers et al. 1995; Liermann and Hilborn 1997). Additionally, Allee effects at the population level may be undetectable when these population data are aggregated across several populations (Frank and Brickman 2000).

The theoretical impact of Allee effects on population dynamics is well established, and numerous mechanisms that might affect offspring production at low abundance have been hypothesized (Stephens and Sutherland 1999; Stephens et al. 1999), including difficulties in mating success (Berec et al. 2001; Rowe et al. 2004; Fagan et al. 2010), cultivation-induced changes to food webs (Walters and Kitchell 2001), and increased predator-related mortality resulting from increased aggregation at low abundance (Peterman 1980; Courchamp et al. 2008).

Our objective here is to quantitatively analyze the relationship between recruitment and spawning stock biomass (SSB) in commercially exploited marine fishes. Analytically, we develop a simple Bayesian hierarchical model to determine how recruitment changes with SSB. The change in recruitment per spawner biomass ($\frac{\text{Recruits}}{\text{SSB}}$) was then modelled for various levels of SSB for 207 stocks. The results show a range of dynamics between $\frac{\text{Recruits}}{\text{SSB}}$ and SSB. Although $\frac{\text{Recruits}}{\text{SSB}}$ increases with decreasing SSB for many species, the S–R dynamics of a substantial number of species exhibits weak compensation, density independence, or an Allee effect as stock size declines.

Materials and methods

Using data collated in the RAM II-SRDB (Ricard et al. 2011), we analyzed commercially exploited teleost marine fishes for which there were more than 10 years of data on both recruitment (thousands of individuals) and SSB (tonnes) and for which stock size and recruitment were estimated by commonly employed fisheries models (e.g., Virtual Population Analysis, Statistical Catch-at-Age). There were 207 stocks (representing 104 species within seven orders) with time series ranging between 10 and 96 years in duration (median of 32 years), resulting in a total of 7290 data points (Supplemental Table S1[1]) with approximately 22% (46) of the stocks having data in all SSB bins. The statistical catch-at-age (SCA) models included in this analysis are fit using an underlying S–R curve, which assumes a compensatory relationship between recruitment and SSB. A complementary analysis was run on the subset of data that excluded the SCA stocks to determine what effect their exclusion might have on the results. This analysis included 99 stocks, representing 59 species within seven orders, and the results of the non-SCA analysis are summarized in Supplementary Figs. S1–S6[1].

The response variable was the number of recruits per kilogram of spawning stock biomass ($\frac{\text{Recruits}}{\text{SSB}}$). SSB is often used as a proxy for a population's total fecundity. Thus, no change in $\frac{\text{Recruits}}{\text{SSB}}$ with changing SSB would suggest that the recruitment was independent of total fecundity (i.e., density independent). In fisheries S–R models, $\frac{\text{Recruits}}{\text{SSB}}$ is assumed to increase as SSB declines, and an Allee effect would be manifested by a decrease in $\frac{\text{Recruits}}{\text{SSB}}$ with declining SSB (Fig. 1).

To facilitate the meta-analysis, the $\frac{\text{Recruits}}{\text{SSB}}$ and SSB metrics were standardized. The ratio of SSB to the historical maximum SSB was grouped into one of seven SSB percentage categories, <10%, 10%–20%, 20%–30%, 30%–40%, 40%–60%, 60%–80%, and 80%–100%, a binning of S–R data that follows that applied by Myers and Barrowman (1996) in their study of the relationship between stock size and recruitment. These particular categories were chosen to provide for more detailed contrasts of the relationship between $\frac{\text{Recruits}}{\text{SSB}}$ and SSB at low abundance while retaining sufficient data within the respective categories to allow for the characterization of general trends throughout the entire range of data. This categorization enables us to estimate the shape of the S–R relationship without the constraints of a parametric model. This method assumes that the maximum biomass observed for each stock is a good estimate of the stock's carrying capacity (K) and that there is equal variance between the SSB categories.

The $\frac{\text{Recruits}}{\text{SSB}}$ data were initially log-transformed to normalize the data. These log-transformed $\frac{\text{Recruits}}{\text{SSB}}$ data were standardized (Z) so that species with highly variable $\frac{\text{Recruits}}{\text{SSB}}$ could be compared in common units of standard deviations from $\overline{\ln\left(\frac{\text{Recruits}}{\text{SSB}}\right)}$:

$$(1)\qquad Z_{ij} = \frac{\ln\left(\frac{\text{Recruits}}{\text{SSB}}\right)_{ij} - \left(\overline{\ln\frac{\text{Recruits}}{\text{SSB}}}\right)_j}{\text{SD}\left(\frac{\text{Recruits}}{\text{SSB}}\right)_j}$$

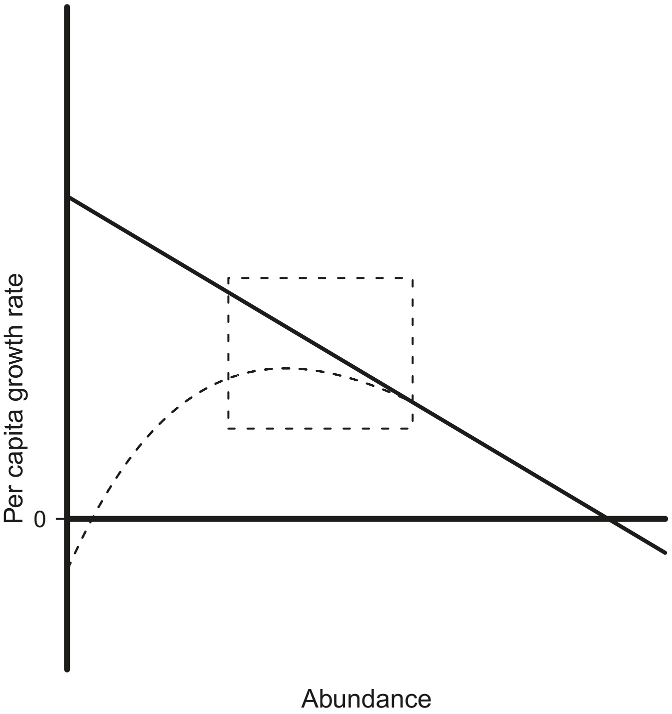
where i represents the individual data point, and j is the species. This analysis tests how deviations of $\frac{\text{Recruits}}{\text{SSB}}$ from the species log-mean $\frac{\text{Recruits}}{\text{SSB}}$ vary with changes in SSB. The standardization also permits comparison between stocks both within and between higher taxonomical levels.

We constructed a multilevel Bayesian analysis of variance (ANOVA) framework for analytical purposes primarily because this modeling approach provides flexibility to develop a model with no strong assumptions about the relationship between $\frac{\text{Recruits}}{\text{SSB}}$ and SSB, thus avoiding problems that can oc-

---

[1] Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/f2012-055.

Fig. 1. Solid line represents theoretical relationship between per capita growth rate and population abundance (density) assuming classical compensatory dynamics (negative density dependence). The *y* intercept represents the maximum rate of population growth, while the *x* intercept is the population's carrying capacity. The dashed line represents a species with an Allee effect; where this line crosses the *x* axis is the "Allee threshold", and below this point population growth is negative. The boxed region represents the "Allee transition region", where classical compensatory dynamics weaken, and transition through apparent density independence to a region of positive density dependence (Allee effect).



cur when attempting to determine the shape of specific S–R models at low abundance (Myers et al. 1995; Liermann and Hilborn 1997). SSB category, the interaction between species and SSB category, and the interaction between order and SSB category were included in the model:

$$(2)\qquad \begin{aligned} y_i &= \gamma_{\mathrm{SSB}} + \delta_{\mathrm{SSB,species}} + \eta_{\mathrm{SSB,order}} + \epsilon_i \\ \delta_{\mathrm{SSB,stock}} &\sim N(\mu_\delta, \sigma_\delta^2) \\ \eta_{\mathrm{SSB,order}} &\sim N(\mu_\eta, \sigma_\eta^2) \end{aligned}$$

where i is an individual data point, y is $Z_{\ln\left(\frac{\mathrm{Recruits}}{\mathrm{SSB}}\right)}$ (hereafter RPS$_Z$; standardized number of log-transformed $\frac{\mathrm{Recruits}}{\mathrm{SSB}}$ is used), γ_{SSB} the mean of each SSB category and was treated as a fixed effect, $\delta_{\mathrm{SSB,species}}$ is the interaction term between species and SSB category, and $\eta_{\mathrm{SSB,order}}$ is the interaction term between order and SSB category. Each interaction in the model was treated as a random variable and assigned a normal distribution with its mean (μ) and variance (σ^2) estimated from the data. The priors for each μ was a zero mean normal prior with σ^2 estimated from the data; for the variance priors an identical vague uniform prior was set on each standard deviation (e.g., $\sigma_\delta \sim U(0,5)$; Gelman and Hill 2007). Models including other taxonomic levels (e.g., stock, genus, family) were also investigated, but these more complex models had to be excluded from further consideration because of data limitations.

Analyses were conducted using R, version 2.14, while Markov chain Monte Carlo (MCMC) sampling was performed using the R2WinBUGS package and WinBUGS version 1.4.3 (Lunn et al. 2000; R Development Core Team 2012). The model was run for 80 000 time steps, with an initial burn-in period of 5000. To eliminate autocorrelation in the MCMC chains, they were thinned, such that only every 200th data point was used. In addition, three separate chains were run to check for nonconvergence of each parameter. Model convergence was assessed via a visual inspection of the MCMC sampling chains and using the Gelman and Rubin convergence diagnostic, $\widehat{R}$. The highest value of $\widehat{R}$ that was observed for any parameter was 1.024, which is less than the threshold value of 1.1, suggesting there is little evidence of nonconvergence for any of the parameters (Gelman and Hill 2007). Posterior predictive checks were used to visually assess the model fit (Supplemental Fig. S8[1]); the model produced reasonable estimates for each species and SSB category within the model (Gelman and Hill 2007). Additionally, a Bayesian *p* value of 0.50 was estimated based on the model results. A well-fit model will have a Bayesian *p* value near 0.5, while a poorly fit model would have Bayesian *p* values skewed towards 0 or 1 (Kèry 2010). Standard residual plots were checked to ensure the error terms were homoscedastic. Finally, a sensitivity analysis was performed to test the influence of individual stocks on the results for each species (Supplemental Fig. S9[1]). In the vast majority of cases, removing one stock had little influence on the model estimates for a species, with exceptions noted in the text.

Bayesian hierarchical models have several advantages over a traditional modelling framework. Using these methods, the variance explained for each hierarchical level can be estimated. This allows for a better understanding of the influence of each level on the model fit (Gelman and Hill 2007). These models also allow for a partial pooling of the results, thus allowing for multiple comparisons without an additional penalty (Gelman et al. 2012). The final advantage is the ability to estimate coefficients for terms at each hierarchical level, allowing for an accurate estimate of the size and direction of any effect at each level in the model (Gelman 2005; Gelman et al. 2012).

Several different comparisons were made when analyzing these data. The primary analysis looked at the contrast between the lowest and second lowest SSB categories on a species by species basis. Ad hoc comparisons were also made among species for which there were obvious trends that the primary analysis did not account for. Strong evidence for either an Allee effect or compensation was based upon the 95% Bayesian credible intervals (BCIs); a second level of weaker dynamics was based on the species' 50% BCI. Negative values for each contrast are indicative of an Allee effect, while positive values reflect compensation.

An additional issue that arises when analyzing these data is that of time series bias (Walters and Martell 2004). However, the effects of time series bias here will be somewhat mitigated by our use of long-term time series that include data at extremely low abundances and across a wide range of fishing mortalities (Walters and Martell 2004). Also, the effect of this bias would tend to increase $\frac{\mathrm{Recruits}}{\mathrm{SSB}}$ at low abundance and reduce $\frac{\text{Recruits}}{\text{SSB}}$ at high abundance, rendering our analysis a conservative test for an Allee effect.

Results

The total variance explained by the model terms accounts for approximately 35% of the total variance in the data (Fig. 2). Overall the SSB term explains 22% of the total variance, the species × SSB interaction explains approximately 12%, while the order × SSB interaction explains less than 1% of the total variance. The pattern of change in RPS_Z with decreasing SSB varies considerably among species and between SSB categories (Fig. 2), while there is little effect of order across the SSB levels (Fig. 3).

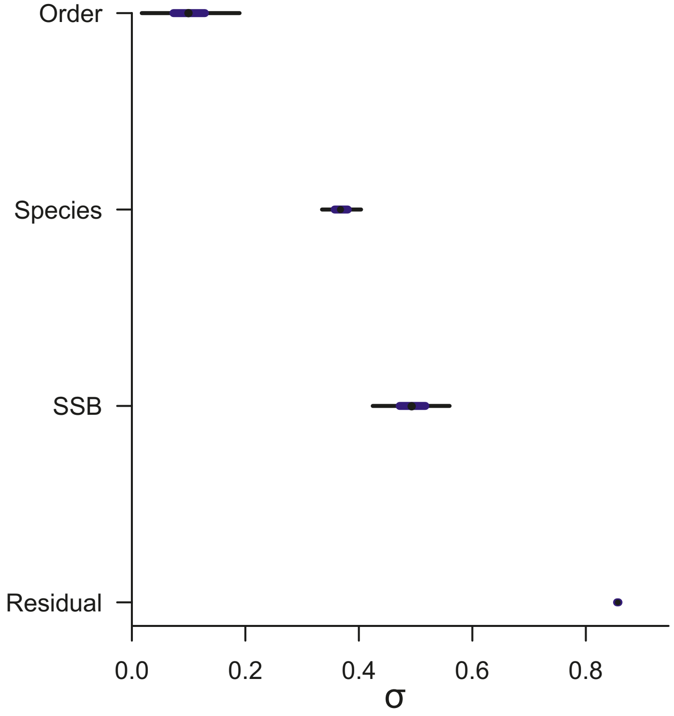
Combining data for all species results in a linear increase in RPS_Z with declining SSB. This is consistent with a linear increase in the RPS_Z vs. SSB relationship as would be predicted from fitting a Ricker S–R model (Fig. 4) on the entire data set. At the lowest SSB level, there is a slight reduction in the rate of increase in RPS_Z. This is the only situation in which the 50% BCIs overlap between any two SSB categories (Fig. 4). This suggests that the influence of compensatory dynamics (i.e., negative density dependence) may have slightly weakened in the lowest SSB category.

A comparison of the raw data and model coefficients ($\delta_{\text{SSB,stock}} + \gamma_{\text{SSB}}$) for two species for which we have the most data (Atlantic cod, *Gadus morhua*; and Atlantic herring, *Clupea harengus*) shows how the relationship between RPS_Z and SSB can differ between species. Although the most dramatic differences are observed in the lowest SSB class (Fig. 5), in which the cod show evidence of an Allee effect, there are also substantive differences at higher relative SSBs. As SSB declined from 60%–80% of maximum SSB to 20%, the herring RPS_Z increased by approximately 0.69 standard deviations (an increase in $\frac{\text{Recruits}}{\text{SSB}}$ from 3.9 to 13.7), whereas for cod RPS_Z increased by only 0.39 standard deviations (an increase in $\frac{\text{Recruits}}{\text{SSB}}$ from 0.53 to 1.0) over the same range. Additionally, for the Atlantic cod stocks the evidence for an Allee effect is largely due to the western Atlantic stocks (Fisheries and Oceans Canada – Northwest Atlantic Fisheries Organization, DFO–NAFO), as only five of the data points in the lowest SSB category come from stocks in the eastern Atlantic (International Council for the Exploration of the Sea, ICES). A subsequent analysis with the cod stocks split into eastern and western stocks indicates that in the western Atlantic, RPS_Z weakens below 30% of maximum SSB, whereas in the eastern Atlantic it is only in the lowest SSB category that compensation in RPS_Z weakens (Supplemental Fig. S7[1]).

In addition to the Atlantic herring, the Pacific herring (*Clupea pallasii*) also exhibit compensatory dynamics at SSBs below 40% (Fig. 3*a*). Notably, two of the other clupeiformes, Peruvian anchoveta (*Engraulis ringens*) and Pacific sardine (*Sardinops sagax*), do not exhibit similar compensatory dynamics at their lowest abundances.

Within the order Gadiformes, the results at low SSB are dominated by both the Atlantic cod and haddock (*Melanogrammus aeglefinus*), which exhibit diverse responses to declines in SSB (Fig. 3*b*). As discussed above, an Allee effect is evident for cod at their lowest historical SSB; the model estimate for cod when RPS_Z is <10% of historical maximum is virtually identical (difference of 0.004) to that for cod abundance levels between 80% and 100% of maximum SSB. The relationship between RPS_Z and SSB is relatively weak in cod, as it increased by only 0.76 standard deviations before an Allee effect becomes evident; this is roughly half of the increase experienced for an average species. The sensitivity analysis indicated that the Allee effect in cod is robust to the removal of any cod stock in the data set, though removal of either of the two stocks with the most data in the <10% SSB category (NAFO-SC-COD3NO and NAFO-SC-COD3M) did increase the modelled RPS_Z estimate in this category (Supplemental Fig. S9[1]). In haddock, RPS_Z is unusually low in the 10%–20% SSB category, followed by a relatively high RPS_Z in the <10% category. Across all SSB categories there is little evidence of a strong relationship between RPS_Z and SSB in haddock, and the sensitivity analysis confirms that these patterns are robust to the removal of any one stock from the analysis.

Fig. 2. The variance explained (σ) by the fixed effect (γ_{SSB}), random effects ($\delta_{\text{SSB,stock}}$, $\eta_{\text{SSB,order}}$), and residual error (ε_i) terms in the hierarchical model. Thick lines represent 50% Bayesian credible intervals (BCIs); thin lines represent 95% BCIs.



The trend for most Perciformes (Figs. 3*c*–3*d*) is similar to that of the overall trend (Fig. 4), although only 9 of 35 perciform species included data for more than one stock. Atlantic bluefin tuna (*Thunnus thynnus*) exhibited the strongest deviation. Its RPS_Z was highest (0.40, SD = 0.18) when the population was between 60% and 80% of its historical SSB. As the population declined from this SSB level, the RPS_Z also declined, (0.05, SD = 0.25) in the 40%–60% SSB category and thereafter remained largely unchanged with further declines in SSB. For this species, the sensitivity analysis (Supplemental Fig. S9[1]) indicates that the high RPS_Z in the 60% to 80% category is strongly influenced by the western Atlantic stock (ICCAT-ATBTUNAWATL). When analysed separately, neither stock (Supplemental Fig. S9[1]; ICCAT-

Fig. 3. Estimated model coefficients of the term $\delta_{\mathrm{SSB,stock}} + \gamma_{\mathrm{SSB}}$ with 50% Bayesian credible intervals sorted by order. (*a*) Clupeiformes, (*b*) Gadiformes, (*c*) Perciformes, (*d*) Perciformes (continued), (*e*) Pleuronectiformes, (*f*) Scorpaeniformes. This figure excludes the orders for which there is data for two or fewer species (i.e., the Beryciformes and Zeiformes).

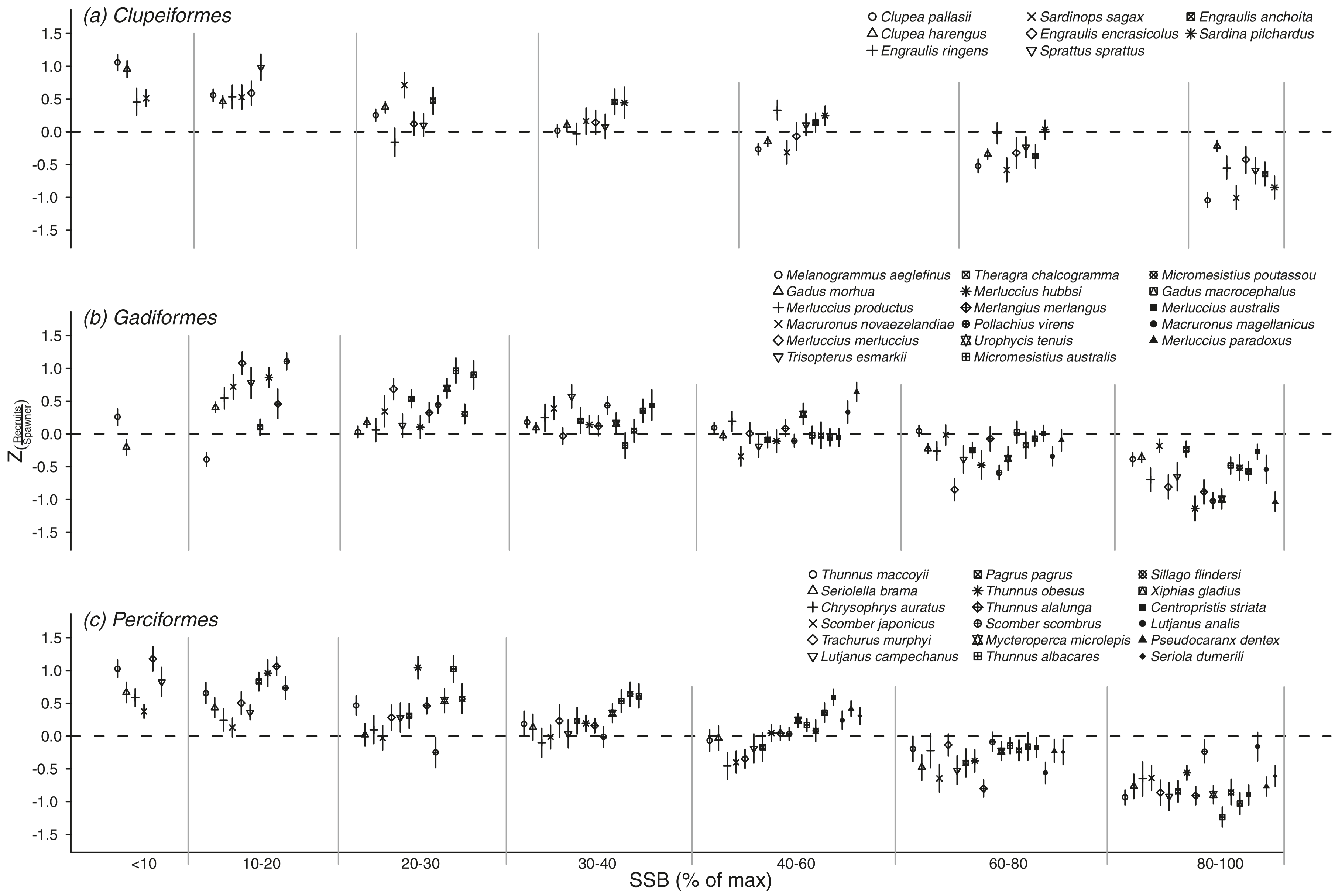


Fig. 3. (*concluded*).

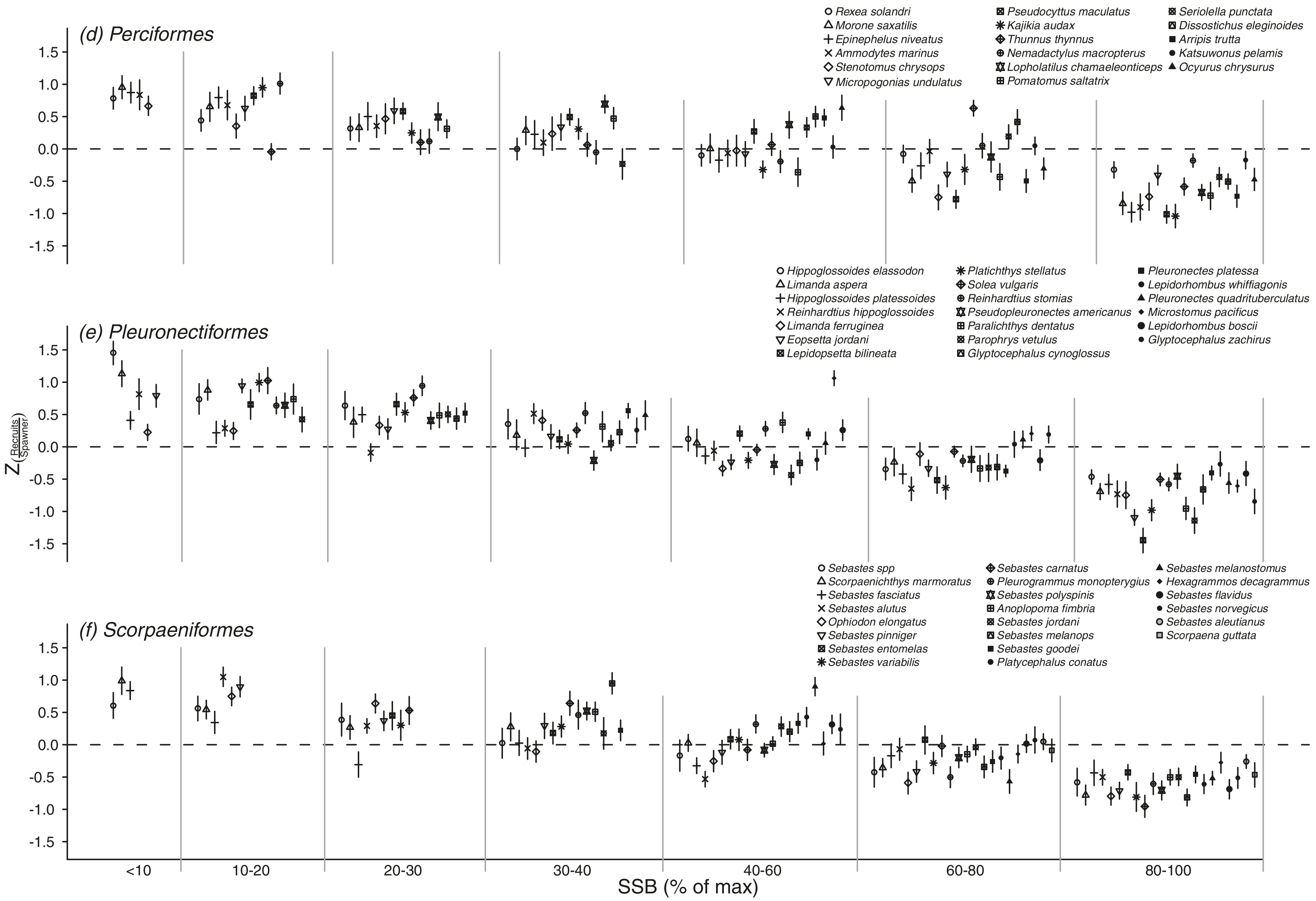


Fig. 4. Modelled relationship between $Z_{\ln\left(\frac{\text{Recruits}}{\text{SSB}}\right)}$ and SSB. Grey points represent individual data points. Model means with 95% Bayesian credible intervals connected with dotted line. A Ricker model based on the entire data set is shown with the solid black line.

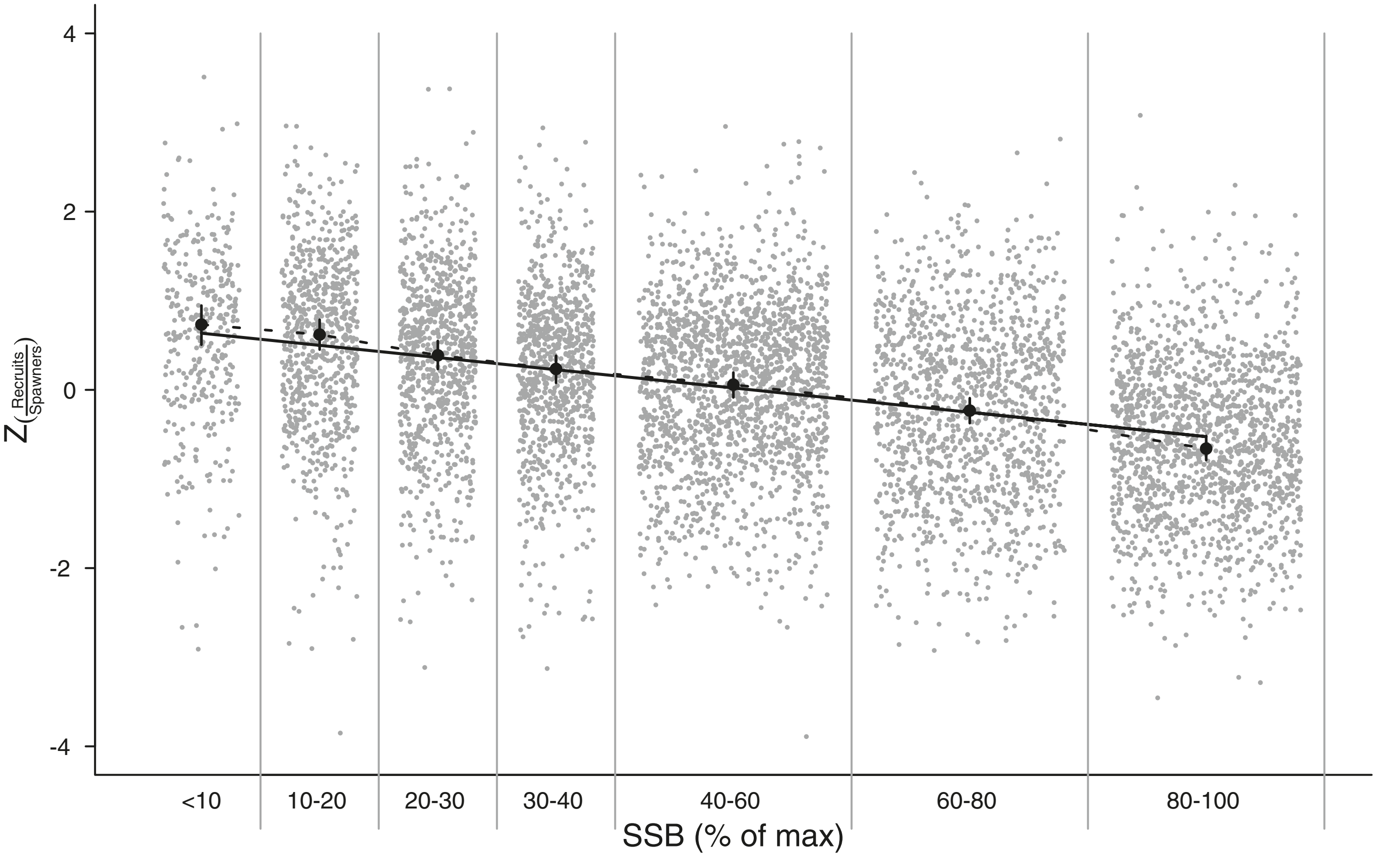
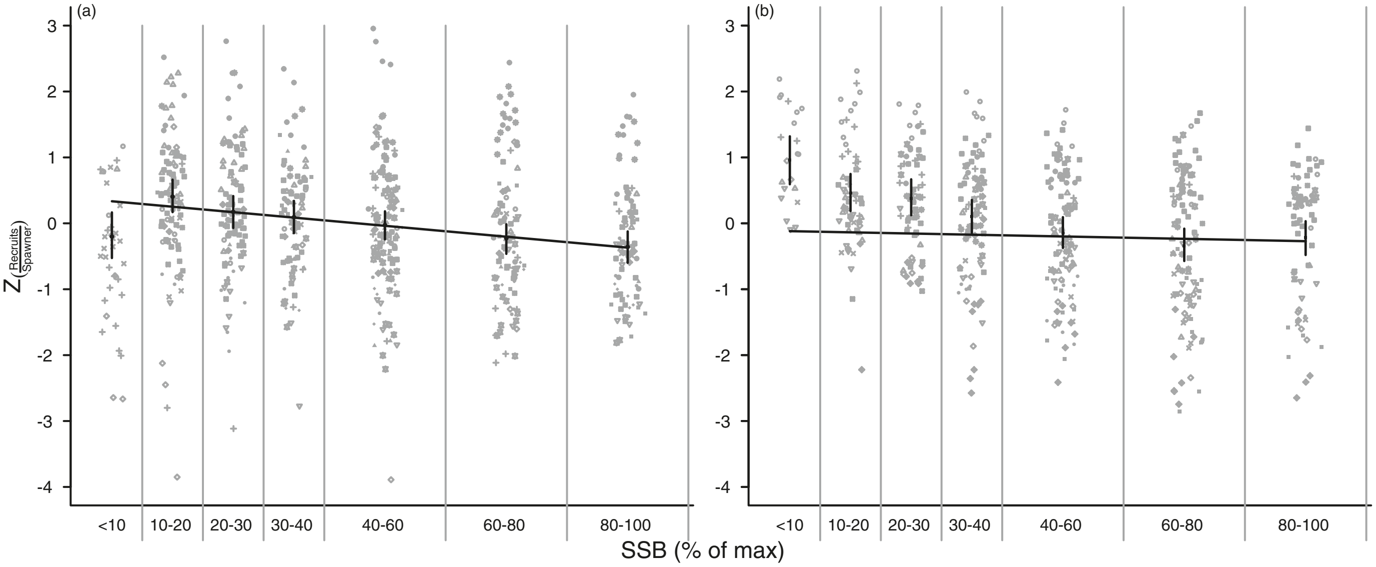


Fig. 5. Estimated model coefficients of the term $\delta_{\text{SSB,stock}} + \gamma_{\text{SSB}}$ for (*a*) Atlantic cod (*Gadus morhua*) and (*b*) Atlantic herring (*Clupea harengus*). Symbols represent individual data points for individual stocks. Model means with 95% Bayesian credible intervals connected with dotted line. A Ricker model based on the data >40% of maximum historic SSB is shown with the solid black line for each species.



ATBTUNAWATL and ICCAT-ATBTUNAEATL) exhibits strong compensatory dynamics at low SSB.

There are several Pleuronectiformes that exhibit a weak relationship between RPS_Z and SSB as SSB declines below approximately 20%–30% of historical maximum. Above this SSB level, the species show a relatively robust increase in RPS_Z with declining SSB (Fig. 3*e*). The Scorpaeniformes are characterized by a large percentage of species having data available for only one stock (16/22). Although there is little evidence of an Allee effect for any scorpaeniform species, there are several species for which there is little evidence of a relationship between RPS_Z and SSB at low abundance (Fig. 3*f*). These include dusky rockfish (*Sebastes variabilis*) and one genus of *Sebastes* sp. (this "population" was only identified to the genus level in the database).

The contrast between the lowest and second lowest SSB categories (based on the model posterior estimates) for each species suggests that there is strong evidence of an Allee effect for only 1 of 104 species at their lowest recorded SSB category. Strong compensatory dynamics is found in 25 species at their lowest recorded abundance (Fig. 6, based on 95% BCIs). There is weak evidence of an Allee effect in another three species and weak evidence for compensation in another 40 species (Fig. 6, based on 50% BCIs). For the remaining 35 species, there is no good evidence of either compensatory dynamics or of an Allee effect. While this may be attributable to low statistical power (because of low sample size and high variability), it also suggests that there is little evidence for compensation in these species when reduced to their lowest historical abundance. Indeed the median difference between the lowest and second lowest recorded SSB categories was negative for approximately 19% of the species (n = 20). Intriguingly, of the 22 species in this analysis whose minimum SSB was in either the 40%–60% or 60%–80% categories, only one had a negative estimate in this analysis (4.5%), and this estimate was only very slightly negative (*Katsuwonus pelamis*, mean difference = –0.02), while of the remaining 82 species that declined below 40% of their maximum SSB, 19 had negative estimates (23%). Additionally, we looked at the trends in the raw data at the stock level. These results largely mirror those found in the model; for example, of the stocks that have declined below 40% of maximum SSB, the lowest SSB category has a lower mean RPS_Z estimate than the second lowest SSB category in 34 (24%, n = 143) of the stocks.

A coarser set of contrasts compared RPS_Z when SSB was below 20% with RPS_Z when SSB was between 20% and 40% of historic maximum. These data suggest that there is little compensation, or a weak Allee effect, in 22% of the species (12/55; note that only 55 of the species had SSB values below 20%). Strong evidence for an Allee effect is not apparent when applying this type of contrast (i.e., all 95% BCIs include 0 when the mean estimate is less than 0). The difference between this and the previous contrast analysis can be attributed to the sharp decline in the lowest SSB category for Atlantic cod (in which strong Allee effects were detected).

In several species this contrast helps clarify the patterns observed in Figs. 3 and 6. For example, while haddock show a strong increase between the lowest and second lowest SSB classification, evidence at the coarser scale suggests there may be a weak Allee effect in this species (Fig. 7). Using this contrast, the dynamics of haddock and Atlantic cod appear similar. Although there are other stocks in which the fine-scale analysis above suggests that the stocks may be experiencing an Allee effect or appear density-independent, this complementary analysis indicates that the RPS_Z for these species did increase significantly in the lowest two SSB classes. However, for these species further reductions in SSB below the 10%–20% category lead to no increase in RPS_Z (e.g., *Eopsetta jordani* and *Engraulis ringens*). This contrast also confirms the observation that Atlantic bluefin tuna RPS_Z exhibits no compensatory recruitment when when SSB is below 40% of maximum.

The analysis on the subset of data that excluded stocks that used an SCA model yielded similar results to the full analysis (Supplemental Figs. S1–S6 and Table S1[1]). The most notable exception is the trend for Atlantic herring at low abundance. At abundances below 40% of historical maximum, there is no strong evidence for compensation in Atlantic herring when looking at the stocks fit without an SCA model (Supplemental Figs. S4–S6[1]). Additionally, the overall estimate of RPS_Z in the lowest SSB category is actually lower than that in the second lowest category when using this subset of data (Supplemental Fig. S3[1]). Of the 59 species in this analysis, 12 had negative estimates (21%), and none of the species (n = 16) whose minimum occurred in either the 40%–60% or 60%–80% categories had negative estimates. Thus, better than 1 in 4 (12/43) species whose abundance declined below 40% of historical maximum had a declining RPS_Z estimate at their lowest historical abundances.

Discussion

Allee effects in marine fishes

Our analysis suggests that the assumption of an increase in $\frac{\text{Recruits}}{\text{SSB}}$ as SSB declines is well founded for many species across much of their historical range in SSB. Overall, there is a steady increase in RPS_Z as SSB declines, although this trend slows at the lowest values of SSB. At their lowest historical abundances, there is an estimated decline in RPS_Z in over 20% of species. While in the majority of cases the difference between RPS_Z in the two lowest SSB categories is not significantly different from zero, this pattern certainly suggests a decline in the strength of compensation. Such a weakening in compensation might be indicative of an Allee transition region (illustrated by the boxed region in Fig. 1; discussed below), where further reductions in abundance would result in a continued slowing of population growth and an inhibition of recovery.

By examining data at the species level, the amount of information available often grows substantially, enabling greater resolution of patterns in $\frac{\text{Recruits}}{\text{SSB}}$ at low abundance, but this could lead to biases in the results based upon the number of time series available for a species (61% of species in the present analysis are represented by a single stock). Species represented by a single stock accounted for 14 of the 26 species classified as having strong dynamics (either compensatory or depensatory), 25 of the 43 species classified with weaker dynamics, and 24 of 35 classified as having density-independent dynamics (68%). Somewhat surprisingly, given the high percentage of single stock species (61%), there is minimal evidence that these species are more likely to be classified as density-independent (68%). Evidence of strong compensation was found in a number of species represented by a single time series. Eleven of the 20 species whose RPS_Z declined from their second lowest to lowest SSB categories were classified as being density-independent based on species represented by a single stock. For these species, there was evidence of a weakening in RPS_Z at low SSB, but the inference was rather weak.

Atlantic cod, a species for which considerable stock-level data were available, exhibited weak compensatory dynamics

Fig. 6. Contrast of $Z_{\ln\left(\frac{\text{Recruits}}{\text{SSB}}\right)}$ between lowest and second lowest SSB category for each species, sorted by order. Negative values represent a lower RPS$_Z$ in the lowest SSB category. Thick lines represent 50% Bayesian credible intervals (BCIs); thin lines represent 95% BCIs. (*a*) Clupeiformes, (*b*) Gadiformes, (*c*) Perciformes, (*d*) Pleuronectiformes, (*e*) Scorpaeniformes. The number of stocks included in the analysis for each species is shown in parentheses after the species name. This figure excludes the orders for which there is data for two or fewer species (i.e., the Beryciformes and Zeiformes).

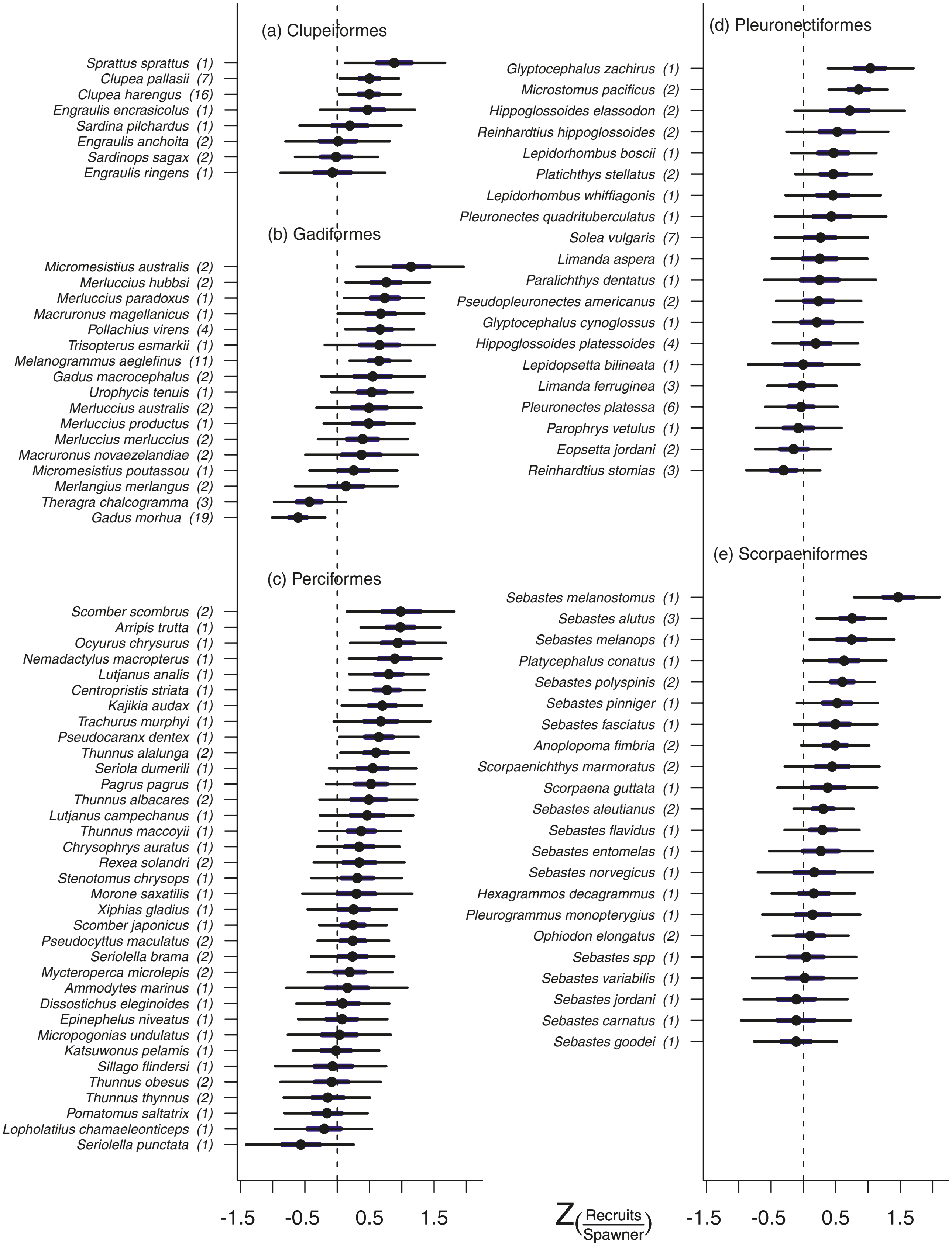
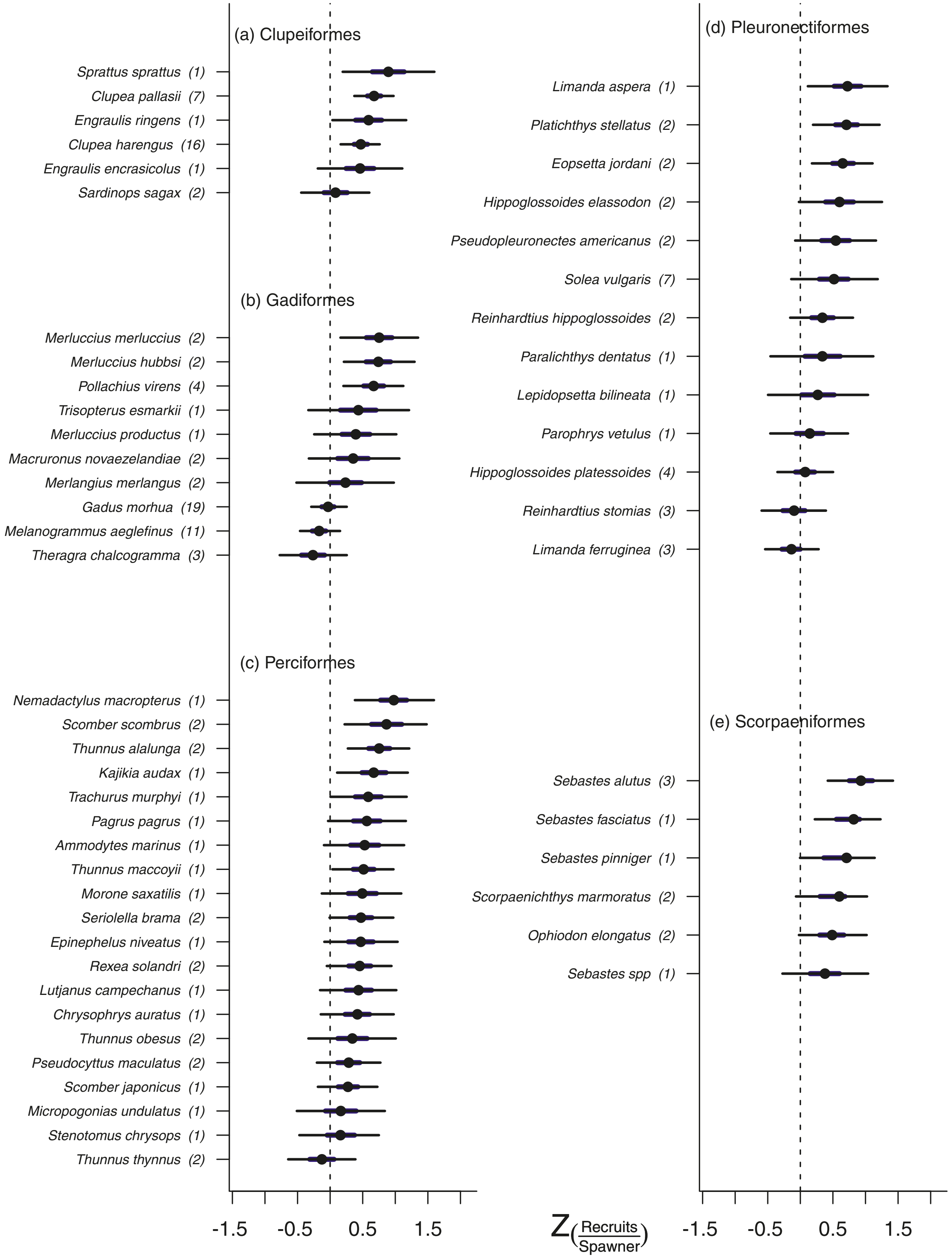


Fig. 7. Contrast of $Z_{\ln\left(\frac{\text{Recruits}}{\text{SSB}}\right)}$ between SSB < 20% and SSB between 20% and 40% for each species sorted by order. Negative values represent a lower RPS$_Z$ in the <20% SSB category. Thick lines represent 50% Bayesian credible intervals (BCIs); thin lines represent 95% BCIs. (*a*) Clupeiformes, (*b*) Gadiformes, (*c*) Perciformes, (*d*) Pleuronectiformes, (*e*) Scorpaeniformes. The number of stocks included in the analysis for each species is shown in parentheses after the species name. This figure excludes the orders for which there is data for two or fewer species (i.e., the Beryciformes and Zeiformes).



at moderate SSBs and the strongest evidence for Allee effects among the species examined here at low SSB. Upon closer inspection of these results, it is clear that the Allee effect is driven by cod stocks in the western Atlantic, where compensation in RPS_Z is weak across all SSB categories, and the Allee effect becomes evident as SSB declines below 30%. In the eastern Atlantic, the cod stocks have not generally been driven to as low abundance as the western stocks, but the evidence suggests that there is compensation in RPS_Z across most SSB categories (although it is approximately 30% weaker than the average species). For these eastern cod stocks, the contrast between the lowest and second lowest SSB categories does suggest a weakening of the RPS_Z–SSB relationship.

Our results suggest that the lack of recovery evident in many of these cod stocks (Hutchings and Rangeley 2011) is related to a decrease in the RPS_Z relationship at low SSB. Our work is consistent with suggestions made by Walters and Kitchell (2001), who, based on a visual inspection of S–R data, concluded that evidence of an Allee effect was strongest in the Gadiformes. Notably, for the two other Gadiformes that have the most data — Atlantic haddock and Alaskan walleye pollock (*Theragra chalcogramma*) — there is little relationship between RPS_Z and SSB when the SSB is below 40% of historical maximum.

The mechanism by which RPS_Z is reduced at low SSB cannot be determined by this type of analysis, but there are a number mechanisms that could result in reproductive Allee effects in Atlantic cod. At low densities, there is experimental evidence to suggest that male cod experience low success and high variability in fertilization rates (Rowe et al. 2004). Additionally, a sex bias in the Northeast Arctic cod population is thought to have contributed to a reduction in total egg production that may have resulted in an Allee effect for this population (Marshall et al. 2006). Sex bias has also been shown to induce Allee effects in sessile marine broadcast spawners by reducing fertilization efficiency (Gascoigne and Lipcius 2004).

The collapse of a fish stock generally results in the truncation of the population's age structure, as fishing generally targets older, larger individuals (Berkeley et al. 2004). With very few older fish surviving, their contribution to recruitment can decline by orders of magnitude, thus substantially increasing the relative contribution to recruitment by younger fish (e.g., northern cod; Hutchings and Myers 1994). Hatching success, length of breeding season, and frequency of batch spawning by first-time spawners are much lower than that of experienced spawners for Atlantic cod (Trippel 1998), and younger spawners may also be less successful than older spawners because of increased variability in recruitment (Hutchings and Myers 1993). Additionally, in longer lived species, the influence of older fish on reproductive rate is greater than that for species with faster life histories (Venturelli et al. 2009). Finally, the number of eggs produced per unit biomass (specific fecundity) has been shown to increase with increasing fish mass, potentially leading to a reduction in recruitment in populations with truncated age structure (Marteinsdottir and Begg 2002).

At the ecosystem level, the lack of recovery in Atlantic cod has been linked to cultivation-induced changes in food webs or an emergent Allee effect (Van Leeuwen et al. 2008; Frank et al. 2011). In these ecosystems, cod would have been a dominant predator, controlling the abundance of various forage fishes. This top-down control of the food web weakens as cod populations are reduced, allowing the abundance of forage fishes to increase by orders of magnitude. Many of these forage fishes feed on planktonic fish larvae, contributing to high mortality of larval cod (Swain and Sinclair 2000).

The other species for which there were considerable data at low SSB were Pacific and Atlantic herring. Herring stock population dynamics appear rather robust to massive declines in abundance, a finding that concurs with conclusions drawn elsewhere (Hilborn 1997; Hutchings 2000; Walters et al. 2008). Nash et al. (2009) attributed strong compensation at low abundance in Atlantic herring to density-dependent effects on mortality during the egg stage, while MacCall (1990) found that predation on eggs could lead to such compensatory dynamics. At high adult abundance, spawning grounds can become saturated with eggs (which are spawned on gravel or on plants), leading to high egg mortality. Conversely, at lower spawner abundance, intraspecific competition is relaxed and egg mortality is reduced. There is also evidence that density-dependent mortality during the larval stage could lead to these patterns in herring (Nash and Dickey-Collas 2005). Finally, in comparison with Atlantic cod, herring species longevity and age at maturity is relatively low. Thus, any fishery-induced truncation in age structure would be less likely to affect reproductive rate (Venturelli et al. 2009).

The Allee effect in some species could also be influenced by environmental regime shifts that negatively affect the number of recruits produced per unit of SSB (Gilbert 1997). These regime shifts can lead to periods of low productivity in which both recruitment and SSB are low. We looked for these trends in several of the western Atlantic cod stocks and found mixed evidence for such a relationship. The strongest support for a regime shift comes from the $\frac{\text{Recruits}}{\text{SSB}}$ of the Gulf of St. Lawrence cod (NAFO zone 4TVn), which declined rapidly in the 1980s when its SSB was at its peak, and while SSB has not recovered since, the RPS_Z since 1993 has been higher than during the peak SSB period of the 1980s. In this stock, these patterns are consistent with a productivity shift in this region, but they are also consistent with a dome-shaped relationship between $\frac{\text{Recruits}}{\text{SSB}}$ and SSB. Evidence for a regime shift in other western Atlantic cod stocks (e.g., NAFO zone 3NO and NAFO zone 3M) is not as strong, but in all of these cases a dome-shaped relationship is found between $\frac{\text{Recruits}}{\text{SSB}}$ and SSB. Additionally, the low SSBs in western Atlantic cod across all stocks did not coincide with environmental conditions known to be particularly detrimental to $\frac{\text{Recruits}}{\text{SSB}}$ in any specific stock. In the western Atlantic, for example, periods of low SSB (late 1980s to present day) have encompassed periods of comparatively warm and cold temperatures (Hutchings et al. 2012). Clearly, a better understanding of the processes (be they biological, environmental, or, more likely, the interaction between the two) that underlie any relationship between abundance and recruitment is vital to the proper management of marine fishes.

Allee transition region

Certain combinations of life-history traits might render some species or populations more susceptible to Allee effects than others (Courchamp et al. 2008). For a given life-history strategy, there is some abundance (range) at which the population dynamics transition from compensatory through density independence and enter the realm in which an Allee effect could be manifested. Determining how different life-history strategies influence the location and shape of this transition, hereafter referred to as the "Allee transition region", has implications for both species conservation and management. Conservation efforts for populations found to be below the Allee transition region would need to be more intensive for a species or population that experienced Allee effect. Alternatively, a population far below its Allee transition region may have such low potential for rescue that limited conservation funds might be better focused on other populations for which management is more likely to be effective. While the magnitude of Allee effect is obviously critical, as a first approximation, knowledge of where classical compensatory population dynamics begin to weaken would be exceedingly useful for both species conservation and fisheries management strategies.

Using S–R relationships to estimate recovery rates

The approach taken in the present analysis does not assume a functional relationship between $\frac{\text{Recruits}}{\text{SSB}}$ and SSB, thus avoiding the difficulties associated with estimating depensation-related model parameters (Myers et al. 1995). An additional advantage is that we are able to differentiate the species-specific shape of the $\frac{\text{Recruits}}{\text{SSB}}$–SSB relationship, which might be spuriously interpreted as simply a poor model fit when using a one-size-fits-all S–R model. Using the relative SSB enables a comparison of populations having very different population sizes, although this assumes that the maximum SSB in the time series is a good proxy for the maximum SSB of a stock. This pooling of data increases the power of the analysis, especially at low spawning stock sizes for which recruitment data are relatively few, but comes at the cost of having to ensure that one does not mask important stock-specific responses.

When rendering predictions about recovery, S–R relationships are often fitted for stocks to estimate their maximum per capita rate of growth at low population size (Myers et al. 1999). This metric is then used to determine how populations will respond to population declines. However, these fits are often performed when there is little information at low abundance (e.g., minimum SSB in available data exceeds 40% of maximum SSB). We show that fitting a classical fisheries model (a Ricker type) would lead to incorrect inferences for at least two species in the present study, indeed those species having the greatest data availability. For Atlantic herring, the model fit would greatly underestimate the RPS_Z at low abundance, while the opposite is evident for Atlantic cod. Based on the Ricker model, one would predict greater compensation in $\frac{\text{Recruits}}{\text{SSB}}$ for cod at low SSB, the opposite of what is suggested when analyzing the entire range of data. Clearly, fitting a population dynamics model to stocks (species) that have not been reduced to low abundance to predict what the dynamics are at low abundance can result in serious errors and incorrect management decisions. For species lacking data at low abundance, a more appropriate approach might be to use species with similar life-history strategies that have been reduced to low abundances to infer putative population dynamics. Additionally, there are few species (bluefin tuna being one notable exception) whose RPS_Z decreases with declining SSB when SSB is relatively high (above 40%–60% of historical maximum), suggesting that the overwhelming majority of species (for which we have data) exhibit compensatory recruitment dynamics even when their SSB has been reduced by approximately 50%.

Previous meta-analysis of the S–R relationship have had limited success in determining the shape of this relationship at low abundance, largely because of a dearth of data at low abundance (Myers et al. 1995; Liermann and Hilborn 1997). Myers et al. (1995) found evidence for depensation in only 3 of 128 stocks, but their data set had very few data at low abundance, which necessarily led to extrapolating curves into regions in which there was no information. Liermann and Hilborn (1997) also found that for the majority of species there is a dearth of strong evidence for either hypercompensation or an Allee effect because the variance in the parameter estimates is so large that it is difficult to determine if a stock is showing evidence for an Allee effect or hypercompensation. The interpretation of our model results suggests that in the majority of species, evidence for compensation is relatively strong at high SSB, but at lower relative SSBs, greater than one in three species show signs of either an Allee effect or density-independent dynamics. While our analysis does not include any salmonids for which Liermann and Hilborn (1997) found the best evidence for an Allee effect, they also suggest that the Pleuronectiformes and Gadiformes exhibited weaker evidence for compensatory dynamics than Clupeiformes. This is similar to our findings in which no clupeiform species show evidence of an Allee effect, while a number of pleuronectiform and gadiform species exhibited evidence of an Allee effect.

Future directions

The present analysis looked solely at the relative changes in $\frac{\text{Recruits}}{\text{SSB}}$ as SSB declines. Although outside the scope of this study, one extension of our work would be to examine absolute changes in $\frac{\text{Recruits}}{\text{SSB}}$ on a stock-by-stock basis to provide estimates of recruitment strength (and associated error) at different levels of abundance. Comparing these estimates with those obtained from the literature would be instructive (e.g., Myers et al. 1999). Additionally, our analysis excluded other potentially relevant covariates (life-history traits, environmental conditions, age structure) that could be included in the model to determine if there is a relationship between these covariates and RPS_Z. Based on the results for the cod and herring, it appears that one covariate worth exploring further is the species reproductive strategy.

The present study provides estimates of the trends in $\frac{\text{Recruits}}{\text{SSB}}$ vs. SSB for many commercially harvested marine fishes. For some species, there is evidence that as SSB declines the relationship between $\frac{\text{Recruits}}{\text{SSB}}$ and SSB weakens, and in some cases an Allee effect is evident. For these species, abundances should be kept above their respective Allee transition regions to minimize the probability of a collapse. In 39 of the 104 species, there is no evidence of compensatory dynamics in the RPS_Z vs. SSB relationship between the lowest SSB and second lowest SSB categories. These relationships can vary substantially within an order, with some species showing strong compensatory dynamics at less than 10% of their historical maximum abundance (e.g., Atlantic herring), while others show no evidence for compensatory dynamics below 30% of historical maximum SSB (e.g., Pacific sardine).

As data at low levels of abundance become increasingly available, it appears that compensation, while strong in some species, is comparatively weak or nonexistent in others, thus providing an explanation for why the recovery of some depleted stocks, despite reductions in fishing mortality, has been considerably slower than what classic models of population growth would otherwise suggest.

Acknowledgements

We are indebted to the many scientists from across the globe for providing the data contained in the RAM Legacy Database. We especially acknowledge Dan Ricard, Coilin Minto, Rebekah Oomen, Paul Debes, and Nancy Roney for their assistance and advice throughout this project. This study was supported by an NSERC Discovery Grant to J.A.H and an NSERC Alexander Graham Bell Scholarship to D.M.K. We are also appreciative of the anonymous referees whose revisions have greatly improved the quality of this manuscript.

References

Berec, L., Boukal, D., and Berec, M. 2001. Linking the allee effect, sexual reproduction, and temperature-dependent sex determination via spatial dynamics. Am. Nat. **157**(2): 217–230. doi:10.1086/318626. PMID:18707273.

Berkeley, S.A., Chapman, C., and Sogard, S.M. 2004. Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. Ecology, **85**(5): 1258–1264. doi:10.1890/03-0706.

Beverton, R., and Holt, S. 1957. On the dynamics of exploited fish populations. Vol. 19 of Fishery Investigations Series II. UK Ministry of Agriculture, Fisheries and Food, London, UK.

Courchamp, F., Berec, L., and Gascoigne, J. 2008. Allee effects in ecology and conservation. Oxford University Press, New York.

de Séligny, J.-F.P., Grainger, R., and Gumy, A. 2010. The State of World Fisheries and Aquaculture (SOFIA) 2010. Food and Agriculture Organization of the United Nations (UN FAO), Rome.

Fagan, W.F., Cosner, C., Larsen, E.A., and Calabrese, J.M. 2010. Reproductive asynchrony in spatial population models: how mating behavior can modulate allee effects arising from isolation in both space and time. Am. Nat. **175**(3): 362–373. doi:10.1086/650373. PMID:20100104.

Frank, K.T., and Brickman, D. 2000. Allee effects and compensatory population dynamics within a stock complex. Can. J. Fish. Aquat. Sci. **57**(3): 513–517. doi:10.1139/f00-024.

Frank, K.T., Petrie, B., Fisher, J.A.D., and Leggett, W.C. 2011. Transient dynamics of an altered large marine ecosystem. Nature, **477**(7362): 86–89. doi:10.1038/nature10285. PMID:21796120.

Gascoigne, J., and Lipcius, R. 2004. Allee effects in marine systems. Mar. Ecol. Prog. Ser. **269**: 49–59. doi:10.3354/meps269049.

Gelman, A. 2005. Analysis of variance — why it is more important than ever. Ann. Stat. **33**(1): 1–53. doi:10.1214/009053604000001048.

Gelman, A., and Hill, J. 2007. Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, New York.

Gelman, A., Hill, J., and Yajima, M. 2012. Why we (usually) don't have to worry about multiple comparisons. J. Res. Educ. Effect. **5**: 189–211.

Gilbert, D.J. 1997. Towards a new recruitment paradigm for fish stocks. Can. J. Fish. Aquat. Sci. **54**(4): 969–977. doi:10.1139/cjfas-54-4-969.

Hilborn, R. 1997. The frequency and severity of fish stock declines and increases. *In* Developing and sustaining world fisheries resources. *Edited by* D.A. Hancock, D.C. Smith, A. Grant, and J.P. Beumer. CSIRO Publishing, Victoria. pp. 36–38.

Hutchings, J.A. 2000. Collapse and recovery of marine fishes. Nature, **406**(6798): 882–885. doi:10.1038/35022565. PMID:10972288.

Hutchings, J.A. 2001. Conservation biology of marine fishes: perceptions and caveats regarding assignment of extinction risk. Can. J. Fish. Aquat. Sci. **58**(1): 108–121. doi:10.1139/f00-228.

Hutchings, J.A., and Myers, R.A. 1993. Effect of age on the seasonality of maturation and spawning of Atlantic cod, *Gadus morhua*, in the Northwest Atlantic. Can. J. Fish. Aquat. Sci. **50**(11): 2468–2474. doi:10.1139/f93-271.

Hutchings, J.A., and Myers, R.A. 1994. The evolution of alternative mating strategies in variable environments. Evol. Ecol. **8**(3): 256–268. doi:10.1007/BF01238277.

Hutchings, J.A., and Rangeley, R.W. 2011. Correlates of recovery for Canadian Atlantic cod (*Gadus morhua*). Can. J. Zool. **89**(5): 386–400. doi:10.1139/z11-022.

Hutchings, J.A., and Reynolds, J.D. 2004. Marine fish population collapses: consequences for recovery and extinction risk. Bioscience, **54**(4): 297–309. doi:10.1641/0006-3568(2004)054[0297:MFPCCF]2.0.CO;2.

Hutchings, J.A., Minto, C., Ricard, D., Baum, J.K., and Jensen, O.P. 2010. Trends in the abundance of marine fishes. Can. J. Fish. Aquat. Sci. **67**(8): 1205–1210. doi:10.1139/F10-081.

Hutchings, J.A., Côté, I.M., Dodson, J.J., Fleming, I.A., Jennings, S., Mantua, N.J., Peterman, R.M., Riddell, B.E., Weaver, A.J., and VanderZwaag, D.L. 2012. Sustaining Canadian marine biodiversity: responding to the challenges posed by climate change, fisheries, and aquaculture [online]. Expert panel report prepared for the Royal Society of Canada, Ottawa, Ont. Available from http://www.rsc.ca/documents/RSCMarineBiodiversity2012_ENFINAL.pdf.

Kèry, M. 2010. Introduction to WinBUGS for ecologists: a Bayesian approach to regression, ANOVA, mixed models and related analyses. Academic Press, Burlington, Mass.

Liermann, M., and Hilborn, R. 1997. Depensation in fish stocks: a hierarchic Bayesian metaanalysis. Can. J. Fish. Aquat. Sci. **54**(9): 1976–1984. doi:10.1139/cjfas-54-9-1976.

Lunn, D., Thomas, A., Best, N., and Spiegelhalter, D. 2000. WinBUGS — a Bayesian modelling framework: concepts, structure, and extensibility. Stat. Comput. **10**(4): 325–337. doi:10.1023/A:1008929526011.

MacCall, A. 1990. Dynamic geography of marine fish populations. University of Washington Press, Seattle, Wash.

Marshall, C., Needle, C., Thorsen, A., Kjesbu, O., and Yaragina, N. 2006. Systematic bias in estimates of reproductive potential of an Atlantic cod (*Gadus morhua*) stock: implications for stock–recruit theory and management. Can. J. Fish. Aquat. Sci. **63**(5): 980–994. doi:10.1139/f05-270.

Marteinsdottir, G., and Begg, G.A. 2002. Essential relationships incorporating the influence of age, size and condition on variables required for estimation of reproductive potential in Atlantic cod *Gadus morhua*. Mar. Ecol. Prog. Ser. **235**: 235–256. doi:10.3354/meps235235.

Munch, S., Kottas, A., and Mangel, M. 2005. Bayesian nonparametric analysis of stock–recruitment relationships. Can. J. Fish. Aquat. Sci. **62**(8): 1808–1821. doi:10.1139/f05-073.

Myers, R.A., and Barrowman, N.J. 1996. Is fish recruitment related to spawner abundance? Fish. Bull. **94**(4): 707–724.

Myers, R.A., Barrowman, N.J., Hutchings, J.A., and Rosenberg, A.A. 1995. Population-dynamics of exploited fish stocks at low population-levels. Science, **269**(5227): 1106–1108. doi:10.1126/science.269.5227.1106. PMID:17755535.

Myers, R.A., Bowen, K.G., and Barrowman, N.J. 1999. Maximum reproductive rate of fish at low population sizes. Can. J. Fish. Aquat. Sci. **56**(12): 2404–2419.

Nash, R., and Dickey-Collas, M. 2005. The influence of life history dynamics and environment on the determination of year class strength in North Sea herring (*Clupea harengus* L.). Fish. Oceanogr. **14**(4): 279–291. doi:10.1111/j.1365-2419.2005.00336.x.

Nash, R.D.M., Dickey-Collas, M., and Kell, L.T. 2009. Stock and recruitment in North Sea herring (*Clupea harengus*); compensation and depensation in the population dynamics. Fish. Res. **95**(1): 88–97. doi:10.1016/j.fishres.2008.08.003.

Peterman, R.M. 1980. Dynamics of native Indian food fisheries on salmon in British Columbia. Can. J. Fish. Aquat. Sci. **37**(4): 561–566. doi:10.1139/f80-071.

R Development Core Team. 2012. R: a language and environment for statistical computing [online]. ISBN 3-900051-07-0. Available from http://www.R-project.org/.

Ricard, D., Minto, C., Jensen, O.P., and Baum, J.K. 2011. Examining the knowledge base and status of commercially exploited marine species with the RAM Legacy Stock Assessment Database. Fish Fish. [In press.] doi:10.1111/j.1467-2979.2011.00435.x.

Ricker, W.E. 1954. Stock and recruitment. J. Fish. Res. Board Can. **11**(5): 559–623. doi:10.1139/f54-039.

Ricker, W.E. 1958. Maximum sustained yield from fluctuating environments and mixed stocks. J. Fish. Res. Board Can. **15**(5): 991–1006. doi:10.1139/f58-054.

Rowe, S., Hutchings, J., Bekkevold, D., and Rakitin, A. 2004. Depensation, probability of fertilization, and the mating system of Atlantic cod (*Gadus morhua* L.). ICES J. Mar. Sci. **61**(7): 1144–1150. doi:10.1016/j.icesjms.2004.07.007.

Shelton, P., and Healey, B. 1999. Should depensation be dismissed as a possible explanation for the lack of recovery of the northern cod (*Gadus morhua*) stock? Can. J. Fish. Aquat. Sci. **56**(9): 1521–1524. doi:10.1139/cjfas-56-9-1521.

Stephens, P., and Sutherland, W. 1999. Consequences of the Allee effect for behaviour, ecology and conservation. Trends Ecol. Evol. **14**(10): 401–405. doi:10.1016/S0169-5347(99)01684-5. PMID:10481204.

Stephens, P., Sutherland, W., and Freckleton, R. 1999. What is the Allee effect? Oikos, **87**(1): 185–190. doi:10.2307/3547011.

Swain, D.P., and Sinclair, A.F. 2000. Pelagic fishes and the cod recruitment dilemma in the Northwest Atlantic. Can. J. Fish. Aquat. Sci. **57**(7): 1321–1325. doi:10.1139/f00-104.

Trippel, E.A. 1998. Egg size and viability and seasonal offspring production of young Atlantic cod. Trans. Am. Fish. Soc. **127**(3): 339–359. doi:10.1577/1548-8659(1998)127<0339:ESAVAS>2.0.CO;2.

Van Leeuwen, A., De Roos, A.M., and Persson, L. 2008. How cod shapes its world. J. Sea Res. **60**(1–2): 89–104. [Spec. Issue SI] doi:10.1016/j.seares.2008.02.008.

Venturelli, P.A., Shuter, B.J., and Murphy, C.A. 2009. Evidence for harvest-induced maternal influences on the reproductive rates of fish populations. Proc. R. Soc. B Biol. Sci. **276**(1658): 919–924. doi:10.1098/rspb.2008.1507. PMID:19033140.

Walters, C., and Kitchell, J. 2001. Cultivation/depensation effects on juvenile survival and recruitment: implications for the theory of fishing. Can. J. Fish. Aquat. Sci. **58**(1): 39–50. doi:10.1139/f00-160.

Walters, C., and Martell, J. 2004. Fisheries ecology and management. 1st ed. Princeton University Press, Princeton.

Walters, C.J., Hilborn, R., and Christensen, V. 2008. Surplus production dynamics in declining and recovering fish populations. Can. J. Fish. Aquat. Sci. **65**(11): 2536–2551. doi:10.1139/F08-170.

Worm, B., Hilborn, R., Baum, J.K., Branch, T.A., Collie, J.S., Costello, C., Fogarty, M.J., Fulton, E.A., Hutchings, J.A., Jennings, S., Jensen, O.P., Lotze, H.K., Mace, P.M., McClanahan, T.R., Minto, C., Palumbi, S.R., Parma, A.M., Ricard, D., Rosenberg, A.A., Watson, R., and Zeller, D. 2009. Rebuilding global fisheries. Science, **325**(5940): 578–585. doi:10.1126/science.1173146. PMID:19644114.