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Renaissance of a caveat: Allee effects in marine fish

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The population dynamics of marine fish at low abundance has long been of interest. One century ago, Johan Hjort drew attention to the importance of understanding "the laws which govern the renewal of the animal population". Integral to the current work on the recovery of collapsed fish stocks is the association between abundance and per capita population growth rate (r), a negative correlation being representative of compensation and a positive correlation indicative of an Allee effect, also termed depensation. Allee effects are predicted to slow the rate, and increase the uncertainty, of recovery. Based on studies having sufficient data at low abundance, the magnitude of depletion experienced by some fish populations appears to have been sufficient to have generated either an Allee effect or a transition from strong to weak (or absent) compensatory dynamics. To a first approximation, empirically based Allee-effect reference points are consistent with suggested thresholds for overfishing and stock collapse. When evaluating Allee effects in marine fish, it is important not to conflate causal mechanism(s) with the pattern between r and abundance; the latter is of greater practical import. An additional caveat is that the longer a population remains at low abundance, the more likely it is that the environment around it will change in ways that are unfavourable to recovery. It might be this "temporal tyranny" of small population size that is most likely to produce an emergent Allee effect and depensatory dynamics in some collapsed marine fish populations.

Keywords: depensation, population growth rate, rebuilding, recovery, reference point, threshold.

A scientific legacy predicated by uncommon breadth

In 1947, Johan Hjort delivered a lecture to the Danish Academy of Natural Sciences entitled "Renaissance of the Individual". It was intended to place his fish research of the early 20th century in the context of his more recent international fisheries and whaling work. The lecture comprised his final publication (Hjort, 1948). In addition to Hjort's personal reflections on the work for which he is best known (Hjort, 1914), the essay is of interest because of the impressive job that he does in weaving together ideas from a broad range of thinkers: Plato, Malthus, Lamarck, Darwin, Goethe. From a social-science perspective, Hjort (1948) emphasizes the importance (the "renaissance") of the individual in the context of both human and fish populations, continuing a narrative evident in his writings in the 1930s (Hjort, 1934, 1935).

Hjort was influenced by a palette of classical ideas atypical of contemporary fisheries science. These ideas contributed to a plethora of interests that sculpted a highly influential legacy to marine fisheries research. Foremost among these are his studies of environmentally driven changes in fish abundance, predicated in particular by his work on Atlantic cod (*Gadus morhua*) and Atlantic herring

(*Clupea harengus*). In 1914, he posited two key ideas (Hjort, 1914, 1948). One of these was that changes in abundance can be greatly influenced by fluctuations in the marine realm (Hjort, 1914), a conclusion stemming from what he had interpreted (Hjort, 1948) to be a lack of association between catches of cod (a presumed metric of abundance) and numbers of fishers (a presumed metric of fishing pressure). A second idea that fish abundance can be significantly influenced by the strength of relatively few year classes, or cohorts, lead him to hypothesize that the primary cause of interannual changes in cohort strength was changes in the abundance of the phytoplankton and zooplankton upon which newly hatched fish larvae depend for food during their "critical period" of early life (Hjort, 1914, 1948).

The question of whether population abundance, in addition to the environment, affects per capita population growth rate (r) is of basic importance to fish population dynamics. Hjort appears to have acknowledged its relevance, noting that "it must be of the greatest importance to ascertain the nature of the laws which govern the renewal of the animal population" (Hjort, 1914). His interest in population dynamical studies matured with his experience on the

International Whaling Commission (Hardy, 1950) and revealed an impressive awareness of recently published research on taxa far removed from fish and marine mammals (Richards, 1928; Klem, 1933). In 1935, for example, he used sigmoidal population growth curves of bacteria to inform changes to, and the threat of overfishing in, the Norwegian whaling industry, noting that "the future of a population may best be predicted by studying the fate of the average individual" whose "standard of life" might best be represented by the "rate of [population] growth" (Hjort, 1934, 1935). Hjort's interest in the renewal of animal populations and of how the population growth rate is related to abundance might be said to have foreshadowed research, initiated half a century later, on factors affecting the recovery of depleted marine fish.

Allee effects and depensation

Few would argue against the assertion that overfishing has been a primary determinant of depletion in marine fish populations (Dulvy *et al.*, 2003). But the question of whether low abundance *per se* is generally of greater influence to population growth following stock depletion than environmental variability is unresolved. One recent study, for example, concluded that although stock abundance was related to stock productivity in almost half of 230 fish populations examined, there were irregular shifts in temporal patterns of productivity that could not be explained by abundance in many stocks (Vert-pre *et al.*, 2013).

Based on Warder Allee's classical work on how "certain aspects of survival values" can increase with density when populations are at low abundance (Allee, 1931, 1938), an Allee effect (often termed "depensation" in the fisheries literature) is "a positive relationship between population abundance (or density) and per capita population growth rate" (Courchamp *et al.*, 1999, 2008; Liermann and Hilborn, 2001; Figure 1). Unfortunately, many definitions exist (Stephens *et al.*, 1999; Lidicker, 2010). Myers *et al.* (1995), for example, defined an Allee effect as the difficulty in finding mates, a definition that conflates cause with pattern. Attempts to partition the fitness consequences of Allee effects can be similarly unhelpful. Some authors (Stephens *et al.*, 1999) distinguish "component" Allee effects (a positive association between a "single" component of fitness and abundance) from "demographic" Allee effects (a positive association between "overall" individual fitness and abundance; in fisheries terminology, mean overall individual fitness is analogous to population productivity, *r*). But this distinction seems unwise from a conservation and management perspective, unless one accepts the doubtful assumption that an increase in one component of fitness automatically leads to an increase in overall fitness. The assumption is unlikely to be true because of the trade-offs ubiquitous among fitness-related traits (Roff, 2002) and the non-depensatory factors that can also affect per capita growth (Liermann and Hilborn, 2001).

An Allee effect is simply a pattern in data. It neither identifies nor implies any particular causal mechanism for generating depensatory dynamics, such as reduced probability of fertilization or finding a mate, impaired group dynamics (e.g. reduced antipredator vigilance), predator saturation, increased incidence of inbreeding or genetic drift, or group conditioning of the environment (Stephens and Sutherland, 1999; Liermann and Hilborn, 2001; Lidicker, 2010). Disentanglement of pattern from causal mechanism would clarify the discussion of Allee effects and its potential importance in marine fish dynamics. Another useful point of clarification is that although an Allee effect can retard the rate and increase the
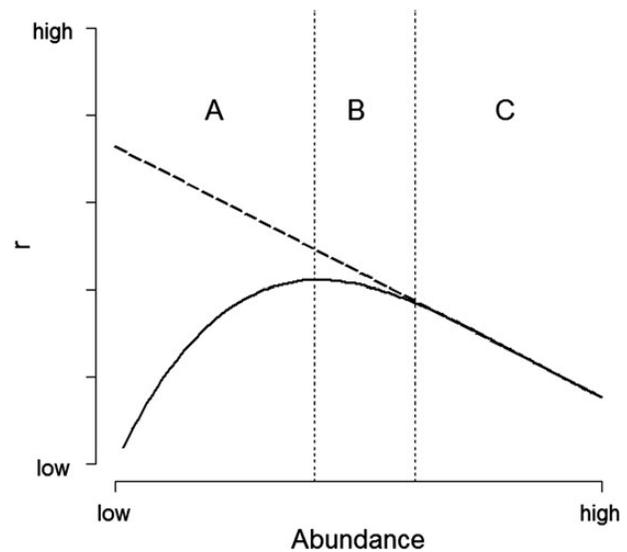

Figure 1. Hypothesized relationship between metrics of *r* (per capita population growth rate) and abundance. The long-dashed line indicates an unchanging level of compensatory population dynamics and is what is typically assumed in fisheries dynamics models. The solid line reflects changes in the pattern between *r* and abundance at different levels of abundance [(A) Allee effect or depensation; (B) Allee transition region (weakening compensation); (C) strong and consistent compensation]. The vertical short-dashed lines partition the three patterns of change.

uncertainty of recovery (Kuparinen *et al.*, in press), it need not prevent recovery.

Why are Allee effects considered unlikely in marine fish?

Allee effects are not considered to be of general importance to marine fish population dynamics, despite the caution that has been expressed in rendering such a position (e.g. Liermann and Hilborn, 1997, 2001; Frank and Brickman, 2000; Hutchings and Reynolds, 2004). There would appear to be several reasons for this conclusion.

The first is that two prominent meta-analyses in the 1990s provided little evidence of depensation. Myers *et al.* (1995) examined stock and recruitment data for 128 marine and anadromous fish populations and estimated the value of a parameter (associated with a modified Beverton–Holt model) intended to describe the curvature of the best-fit model to recruitment data at low levels of stock abundance. Of the 26 datasets considered to have sufficient power to detect depensation, only three of them did so, and the only one of these three that was a marine species was the Icelandic spring-spawning herring.

The second meta-analysis employed a Bayesian hierarchical modelling approach to the same dataset. Liermann and Hilborn (1997) reported that the probability distributions of a parameter they used to detect an Allee effect were sufficiently broad to lead them to conclude that one cannot discount the possibility that fish population dynamics are affected by depensation. In other words, difficulties in detecting depensation should not lead one to conclude that depensatory dynamics are rare and unimportant (Liermann and Hilborn, 2001).

In addition to the non-confirmatory nature of these two meta-analyses, there are comparatively few experimental or single-species studies of Allee effects in marine fish, either because these effects have been little-studied or because of a bias against publishing "negative" results (the latter seems unlikely, given that such analyses are prevalent in the non-fisheries literature, e.g. Sæther et al., 1996; Gregory et al., 2010).

General reviews, for example, have documented little evidence of the causal mechanisms of Allee effects in marine fish, e.g. Gascoigne and Lipcius (2004) and Lidicker (2010). Although the impression left by Kramer et al. (2009) is that Allee effects have often been found in fish, the studies themselves were not cited, rendering the basis for the assertion, and the extent to which they apply to marine fish, unclear. Berec et al. (2006) and Gascoigne et al. (2009) cite potential examples in Atlantic cod: laboratory evidence for reduced fertilization success at low densities (Rowe et al., 2004) and altered interspecific interactions (predation, competition) concomitant with low adult abundance (Walters and Kitchell, 2001). The latter, sometimes termed a "cultivation effect", has been linked to slow or absent recovery in cod (Swain and Sinclair, 2000; Frank et al., 2011) and implicated as a potential source of Allee effects in white hake (*Merluccius capensis*; Vergnon et al., 2008). Liermann and Hilborn's (2001) review identified two studies of marine fish (Brock and Riffenburgh, 1963; Steele and Henderson, 1984) that provide circumstantial evidence that increased abundance reduces predation mortality in schooling, pelagic fish. And Stephens and Sutherland's (1999) sole example of a marine fish draws attention to laboratory work on pollock (*Pollachius virens*) which suggests that these advantages to schooling might also apply to demersal species (Rangeley and Kramer, 1998).

Absence of evidence does not constitute evidence of absence

As alluded to previously, a third reason for the perceived lack of importance of Allee effects in marine fish can be attributed to data limitations. Liermann and Hilborn (1997) cautioned that high data variability and few observations at low spawner levels might contribute to the perception that depensation is not possible in marine fish. Myers et al. (1995) attempted to account for these data limitation by estimating the statistical power of detecting depensation in their data. Of 128 time-series, only 15 were deemed to provide sufficiently high statistical power in marine fish (11 other datasets having sufficient power represented two species of salmon). After detailing what they perceived to be computational problems in how Myers et al. (1995) had estimated statistical power, Shelton and Healey (1999) concluded that depensation will be difficult to detect unless the depensation effect, as reflect by Myers et al.'s (1995) parameter, is substantive. They also noted the inherent difficulty in detecting depensation when there is a paucity of spawning-stock biomass (SSB) data at low stock sizes and when time-series are comparatively short [i.e. less than 30 years; Myers et al. (1995) and Liermann and Hilborn (1997) applied a 15-year minimum to the data they analysed].

In a similar vein, based on a meta-analysis of time-series abundance data for insects, birds, mammals, and fish, Gregory et al. (2010) reported that support for models of both negative (compensation; Figure 1) and positive (Allee effect) density feedback increased with data availability at low population sizes. Another caveat related to data quality is that stock and recruitment data aggregated across multiple substocks can fail to detect Allee

effects, although each of the substocks exhibits them (Frank and Brickman, 2000).

Allee effect thresholds and the Allee transition region

In an attempt to overcome some of these data limitations, Keith and Hutchings (2012) analysed a larger dataset (207 marine fish populations) that included longer average time-series for each stock (median period was 32 years) and that encompassed periods of time during which many stocks had remained at low stock levels, thus increasing the number of datapoints at abundance levels at which Allee effects might be evident. Based on the results of a Bayesian hierarchical model, they reported that: (i) many stocks (such as those of Atlantic herring) exhibit strong compensatory population dynamics, meaning that recruits-per-spawner (a strong correlate of r) always increased as SSB declined; (ii) others exhibit little or no compensation at low stock size; and (iii) some stocks for some species exhibit patterns in stock size and recruitment consistent with the pattern of an Allee effect.

The meta-analysis by Keith and Hutchings (2012) provided some guidance in identifying a "threshold" level of abundance below which an Allee effect, if present, is likely to be detected. When compensation was weak or absent and when Allee effects were detected, they found that SSB was usually less than 10% of the maximum value observed (SSB_{max}; Figure 2). This is not unlike the "threshold" values (although these lacked an empirical basis) used by Fowler and Baker (1991) in their analysis of Allee effects in large mammals (also 10%) and by Sæther et al. (1996) in their analysis of birds (15%). If a $< 0.10\ SSB_{max}$ criterion had been applied to the dataset used by Myers et al. (1995) (and by Liermann and Hilborn, 1997), very few time-series would have met this data restriction. Of the 15 time-series for marine fish for which statistical power was deemed sufficient to detect depensation (Myers et al., 1995), only 8 (representing four species) contained at least five SSB estimates at $< 0.10\ SSB_{max}$ (four time-series contained no SSB data at $< 0.10\ SSB_{max}$). By comparison, in the temporally
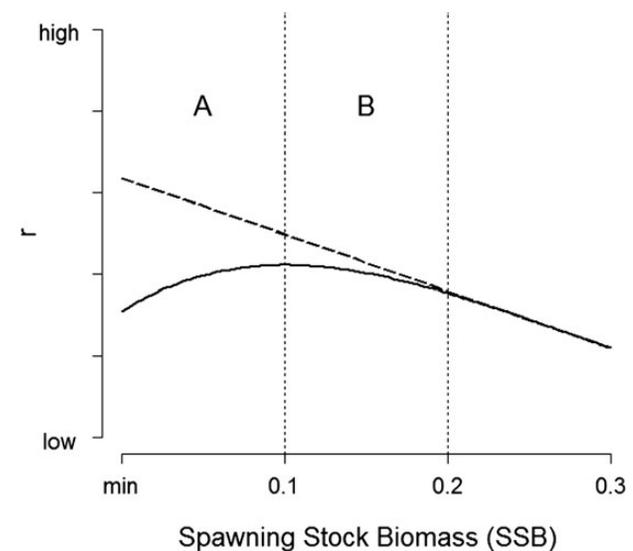

Figure 2. Relationships between r (per capita population growth rate and related to recruits per spawner) and SSB, showing suggested abundance thresholds for the Allee effect (A) at 0.10 SSB_{max} and the Allee transition region (B) at 0.20 SSB_{max}.

and spatially expanded data analysed by Keith and Hutchings (2012), SSB estimates of <0.10 SSB_{max} were available for 26 species, 19 of which included at least 5 datapoints.

In addition to documenting an Allee effect in some populations, the analysis by Keith and Hutchings (2012) yielded the disconcerting observation that compensatory population dynamics at low stock sizes were not evident in 39 of 104 marine fish species. As reflected by recruits per spawner (R/S) increasing very slowly or not at all with declining SSB (Figure 1B), a lack of strong compensation was not always manifested by an Allee effect, as would be demonstrated by R/S declining with declining SSB (Figure 1A). This outcome suggests that, for some populations, there is an abundance threshold greater than the Allee-effect threshold at which populations enter what Keith and Hutchings (2012) termed an "Allee transition region" (Figure 1B). An Allee-transition threshold would identify an abundance below which the population dynamics of some populations transition from strong compensatory dynamics through density-independent dynamics and, potentially, to levels of abundance at which an Allee effect could be manifested.

Among those stocks for which there was evidence of an Allee transition phase, the weak or absent compensatory dynamics characteristic of the transition region were generally realized at stock sizes less than 0.20 SSB_{max} (Keith and Hutchings, 2012; Figure 2).

Allee effect reference points

Reference points are increasingly used to guide many elements of fisheries management and conservation plans (Hilborn and Stokes, 2010). The SSB thresholds identified above might be described by more generic thresholds, particularly if they were estimated in relation to a commonly applied reference point, such as SSB_{msy}, the SSB at which the maximum sustainable yield is predicted to be obtained. One might argue that SSB_{max} is problematic because it might not be known how representative it is of the unfished biomass or carrying capacity (K) of a given stock. Under the assumption that it underestimates K (fisheries for many stocks often having preceded the collection of SSB data), the thresholds identified here—low levels of relative abundance that should be avoided—would be conservative insofar as a reduction to less than 10% of SSB_{max} would render it highly probable that abundance has declined to less than 10% of K.

The RAM Legacy Stock Assessment Database (Ricard *et al.*, 2012; http://depts.washington.edu/ramlegac/wordpress/) includes data on SSB_{msy} and SSB_{max} (maximum observed value of SSB) for more than 130 marine fish stocks ($n = 135$ at the time of analysis). Excluding the 11 estimates of SSB_{msy} in the database that exceed SSB_{max}, on average, $SSB_{msy} = 0.39\ SSB_{max}$. To a rough first approximation (clearly more sophisticated analyses are possible), the Allee-effect abundance threshold suggested above (0.10 SSB_{max}) would correspond to 0.26 SSB_{msy}, and the suggested Allee-transition threshold (0.20 SSB_{max}) would correspond to 0.52 SSB_{msy} (Figure 3).

Interestingly, these Allee-effect and Allee-transition reference points are not dissimilar to those applied elsewhere for somewhat similar purposes. Neubauer *et al.* (2013), for example, defined a collapsed stock as one that had declined to less than 0.20 B_{msy}. Their work also indicated that collapsed stocks have considerably longer, and highly uncertain, recovery periods when compared to stocks that have declined to lesser degrees. Many jurisdictions, such as the United States and Australia, use 0.50 B_{msy} as the threshold that identifies overfishing (Hilborn and Stokes, 2010).
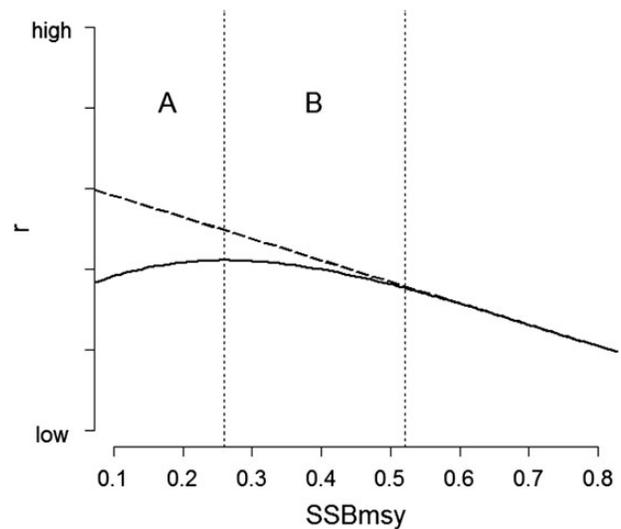

Figure 3. Relationships between r (per capita population growth rate and related to recruits per spawner) and SSB_{msy} (SSB corresponding to maximum sustainable yield), showing suggested reference points for the Allee effect (A) at 0.26 SSB_{msy} and the Allee transition region (B) at 0.52 SSB_{msy}.

The Allee-effect reference points suggested here provide empirical strength, from a population dynamical perspective, to the (arguably) arbitrary reference points articulated elsewhere for stock collapse and overfishing. That is, some stocks that have declined below 0.20 B_{msy} (collapse) and 0.50 B_{msy} (overfishing) might be likely to face increased probabilities of realizing an Allee effect or of entering an Allee transition region, respectively, and thus experiencing reduced probabilities of recovery. Links between fisheries reference points and population-depletion criteria applied by conservation organizations, such as the IUCN (World Conservation Union), have been examined comprehensively elsewhere (Dulvy *et al.*, 2005; Davies and Baum, 2012) and the utility of using both to assess conservation status is amply supported by these studies.

Closing points

There is evidence in some, but not all, marine fish populations that compensatory density-dependence weakens when abundance declines to very low levels (Keith and Hutchings, 2012). Such a weakening in the strength of compensation will increase the uncertainty of recovery in depleted populations, underscoring the diminished ability of small populations in general to persist and grow in the presence of environmental stochasticity (Lande, 1993).

When evaluating the potential importance of Allee effects on the population dynamics of marine fish, the following points merit consideration.

First, mechanisms underlying Allee effects should not be conflated with the pattern of an Allee effect. It is the way in which r changes with abundance at low population sizes that is of primary importance to fishery rebuilding, population recovery, and conservation status, not whether one mechanism or another is responsible for the pattern (although the latter is clearly worth exploring in its own right).

Second, an Allee effect need not prevent recovery (unless, of course, r is negative). Rather, it is predicted to retard the rate of,

and increase the uncertainty associated with, recovery (Kuparinen *et al.*, in press).

Third, the abundance thresholds and reference points for Allee effects and Allee transition regions suggested here lend support to reference points identified elsewhere for overfishing and population collapse, providing additional reasons to fishery managers for why these regions of fish stock abundance should be avoided.

Fourth, it seems important to distinguish the passing of a threshold or reference point pertaining to an Allee effect from the period that a population spends at such low abundance (note that persistence at low abundance can be a product of low *r* coupled with environmental stochasticity; it need not reflect the attainment of a stable equilibrium). It might well be that the passing of an Allee-effect threshold by a population for a short period, relative to that population's generation time, will in itself not be sufficient to generate a reduced rate of recovery.

But logic dictates that the longer a collapsed population remains at low abundance, the more likely it is that the environment around it will change, quite possibly in ways that are unfavourable to the growth and the recovery of the depleted population (Swain and Sinclair, 2000; Brander, 2005; Benoît and Swain, 2008; Swain, 2011; Audzijonyte *et al.*, 2013). Changes in the abundance of interacting species to which an increasingly depleted population becomes increasingly vulnerable can lead to what has been termed an "emergent" Allee effect (*sensu* Courchamp *et al.*, 2008; Hutchings and Rangeley, 2011). One example of an emergent Allee effect would be reductions in *r* of a depleted population resulting from increases in predator abundance to which the prey's *r* would not otherwise have been affected if the predator abundance had not increased (see Swain, 2011, for a potential example). This is one of the tyrannies of small population size. The longer a population remains small, the longer, and more uncertain its recovery (Lande, 1993; Neubauer *et al.*, 2013), particularly when Allee effects are present (Kuparinen *et al.*, in press). Methodologically, a stock:recruitment analysis may be of limited utility as a means of detecting depensation if emergent Allee effects increase adult mortality (thus reducing *r*) as SSB declines, but do not affect *R/S*.

Hjort's (1914) attention to understanding the factors affecting the renewal of marine fish populations, notably within the context of the population growth rate (Hjort, 1934, 1935), has particular import to the study of recovery in depleted marine fish, a subject of enquiry that has increased during the past 20 years (e.g. Hutchings, 2000; Worm *et al.*, 2009; Murawski, 2010; Lotze *et al.*, 2011; Neubauer *et al.*, 2013). Among the hypothesized correlates of recovery, a key one pertains to population dynamics at low abundance. The slow or absent recovery currently observed for some marine fish populations provides an appropriate empirical template against which a renaissance of the caveat of the Allee effect might be fruitfully considered.

Acknowledgements

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