Allee effects and their potential relevance to exploited Abalone Populations

Michelle De Decker, Charlie Edwards & Doug Butterworth
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What is an Allee effect?

The Allee effect refers to the per capita growth rate of a population *r* (i.e. the increase in population size per individual present) and how this property changes at low population sizes. As a population is reduced below it's carrying capacity, it is generally assumed that *r* will increase. However at very low levels, further reductions in population size may lead to *decreases* in *r*, so that recovery of the population is impeded. This is the Allee effect. In extreme cases *r* may even become negative, leading to population collapse.

Allee effects and human impacts on marine systems.

Most marine taxa have planktonic larvae that spend days to months in the water column and are therefore capable of wide dispersal. Marine systems have therefore generally been considered to be large, so that Allee effects are unimportant. However, for many species, larvae may be retained locally, or have fragmented or dramatically reduced populations rending them susceptible to Allee effects.

Populations that are potentially susceptible to Allee effects have evolved mechanisms to avoid them (e.g. large eggs, long-lived sperm, and aggregation or spawning synchrony in the case of broadcast spawners). However, top-down predation by humans has recently (in evolutionary terms) become a dominant force in almost every marine system, so that population sizes may have been reduced to levels that are unprecedented in pre-exploitaton 'natural' systems.

There is also a new type of human-induced Allee effect, the anthropogenic Allee effect, which characterizes situations where exploitation rates increase as population declines. When rarity is associated with value, high exploitation costs of the few remaining individuals are no longer an economic constraint, and ecological extinction can precede economic extinction. Rare species are considered more valuable and would consequently suffer enhanced exploitation, and become even rarer.

Even if eventually halted, exploitation can bring the population close to or even below the Allee threshold corresponding to the natural Allee effect. Several species of California abalones could be a typical example of stocks being unable to bounce back even after complete cessation of fishing, because of an unsuspected Allee effect. More than 10 years after closing the fishery, it appears that an overlooked mating-related Allee effect (abalones as broadcast spawners need to exceed a critical

density for an efficient fertilization) might have combined with an anthropogenic Allee effect to drive the population below the levels that were then considered safe for exploitation.

A clear example of Allee effects in natural gastropod population is provided by the Alaska Fisheries Science Centre. They conducted surveys of adult density, reproductive behaviour, and spawning in natural populations of Caribbean queen conch Strombus gigas at 2 locations in the Excuma Cays, Bahamas, to test for Allee effects. Mating never occurred when density was <52 conch ha^{-1}, and spawning never occurred at <48 conch ha^{-1}, clearly demonstrating the operation of depensatory mechanisms. Reproductive behaviour then increased rapidly to asymptote at densities near 200 conch ha^{-1}. Heavily exploited populations of queen conch in the Caribbean have been slow to recover despite fishery closures. Failure to recover could result from spawning stock densities that are reduced to the point at which Allee effects begin to operate on reproductive behaviour.

A combination of laboratory and field experiments with commercial abalone species *Haliotis laevigata* showed that fertilization may be a limiting factor in some exploited populations when distances separating spawning individuals are too large. The effects of gamete age, gamete concentration, and gamete contact time in the laboratory were used to model fertilization success in situ and compared with experimental fertilization rates in the field. Highest fertilization rates in vitro (80%) were found for sperm concentrations in the range of 1×10^4 to 1×10^6.mL^{-1}. fertilization rates of 48 ± 1.7% (95% CI) at 16m downstream, agreeing closely with the rates predicted by the model. Recruitment failures reported for South Australian populations of *H. laevigata* have occurred when densities fell below ~0.3 animals.m^{-2}, or mean nearest-neighbour distances between 1 and 2 m. This density corresponds well to critical nearest-neighbour distances for fertilization success. Stocks at higher densities are predicted to have higher fertilization rates (~90%) such that fertilization success is not a factor limiting recruitment.

Allee effects in broadcast spawners

A component Allee effect refers to the mechanism by which an Allee effects acts, should the population size be reduced to the required level. Many marine taxa possess a clear-cut component Allee effect in their reproductive system: they are sessile or semi-sessile broadcast spawners. Fertilization success of eggs depends on the concentration of sperm in the water column. The proportion of eggs fertilized declines exponentially with the distance of the female downstream from the nearest male (Fig. 5). At the nearest-neighbour distances of <1m, models predict that <0.1% of eggs will be fertilized under high turbulence, although fertilization efficiency varies depending on the taxon and the environment. Numerous marine invertebrate taxa are broadcast spawners. Most species where the adults are usually sessile, such as corals, anemones, ascidians and sponges, have no other option for sexual reproduction, although they usually also reproduce clonally and may be self-fertile.

However component Allee effects may never actually impact the demography of the population due to compensatory mechanisms. In urchins, competition often results in a smaller mean body size rather than higher mortality, since most echinoderms can shrink if resources are scarce. In *Diadema antillarum*, the increase in gamete production by larger individuals at low density seems to offset the reduction in fertilization efficiency, such that individual reproductive output remains broadly similar across a wide range of densities. In addition, many taxa have evolved ecological and physiological mechanisms to avoid sperm limitation, so in natural (non-experimental) systems, may be

well adapted for efficient fertilization even at low density. Moreover, various invertebrates show negatively density dependent predation mortality at low population densities which could offset component Allee effects in reproduction.

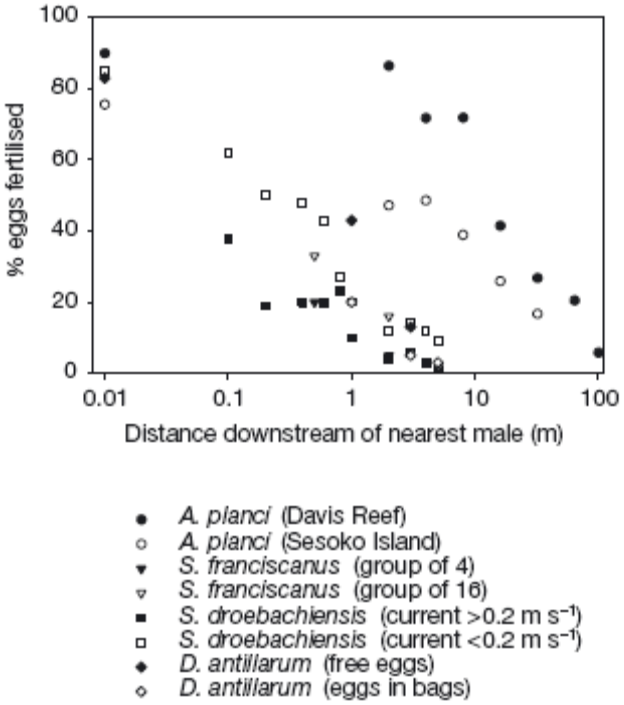

Fig. 5. Fertilisation success in echinoderms, showing a general trend of exponential decline in the proportion of eggs fertilised with distance downstream of the nearest male. Data from: Babcock et al. 1994 (crown of thorns starfish *Acanthaster planci*); Levitan et al. 1992 (red sea urchin *Strongylocentrotus franciscanus*); Pennington 1985 (green sea urchin *S. droebachiensis*); Levitan 1991 (Caribbean long-spined sea urchin *Diadema antillarum*)

Populations of many broadcast spawners have suffered dramatic reductions in density through exploitation. There has been heavy exploitation of sea urchins, sea cucumbers, Eastern oysters and abalone, reducing populations to levels that seem to be unprecedented in recent or even geological history. There are several examples where populations subjected to such extreme exploitation have collapsed rapidly (e.g. abalone, sea urchins), but is there evidence that a component Allee effect from broadcast spawning has had demographic consequences? Unfortunately direct evidence for this is sparse.

In abalone, a decreasing proportion of reproductive adults participate in spawning aggregations in heavily fished, low density populations. Abalone species have been serially depleted along the NE Pacific coast, demonstrating the rapidity with which each population collapsed after the fishery focused on it (Fig. 6)

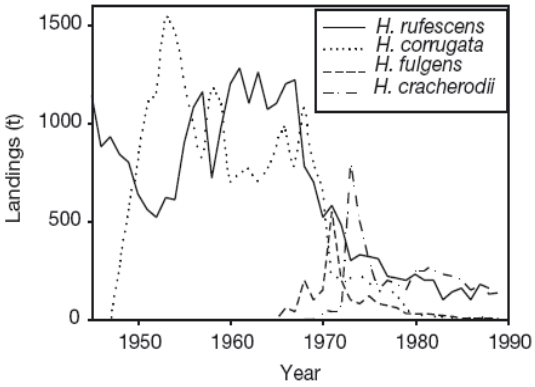

Fig. 6. Population size of abalone species (red abalone *Haliotis rufescens*; pink abalone *H. corrugata*; green abalone *H. fulgens*; black abalone *H. cracherodii*) in California. Note the pattern of serial collapse as the fisheries move on to each species in turn. Red are the preferred species for the fishery, followed by pink, green and black. Data from Parker et al. 1992, Tegner et al. 1992

To test whether this was due to Allee effects, the landings of red and pink abalone were examined. If landings were assumed to be proportional to population size, the ratio of landings at time t+1 to landings at time t is an estimate of the average population growth over the year. The relationship between estimated population growth rate and landings is significantly positive (Figs. 7&8), suggesting that population growth rate increases with population size. This is suggestive of an Allee effect, although it could also be a function of changes in effort.

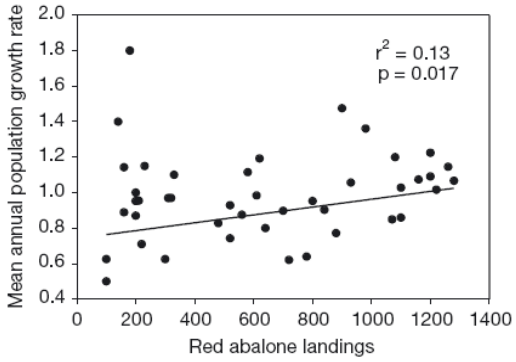

Fig. 7. Mean annual population growth rate of red abalone, on the assumption that landings are proportional to the population size (ratio of landings at time $t+1$ to landings at time t) vs landings in metric tonnes. A positive slope indicates the possibility of an Allee effect, with an Allee threshold (population growth rate = 1) at the population level which provides landings of ~1200 t

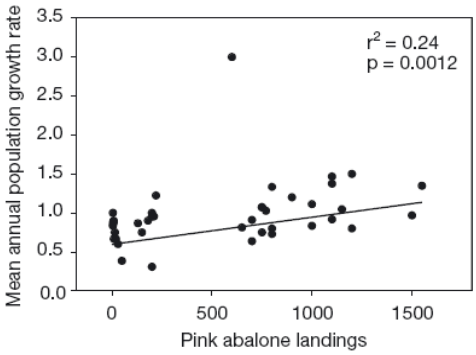

Fig. 8. As for Fig. 7 but for pink abalone. Again, a positive slope indicates a potential Allee effect with a threshold at landings of ~1200 t

Conclusion

Exploitation therefore has the potential to render populations very vulnerable to collapse when Allee effects are present. This review of empirically based analyses on Allee effects in diverse marine species revealed numerous suggestive observations, but very little firm evidence. The failure to demonstrate Allee effects convincingly in marine populations might be methodological, since there is a lack of clear understanding on the part of many ecologists as to the precise definition of Allee effects. Also, given the usual time scale for scientific research the presence of Allee effects may be difficult to verify in long-lived exploited species such as abalone.

Does this mean Allee effects can be dismissed as unusual or insignificant in marine populations? Allee effects can have major consequences for population dynamics, sustainable exploitation and management. The potential population consequences of mechanisms for component Allee effects remain unexplored in most marine species. This limits both our ecological understanding and the probable success of conservation for marine species.

References

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