Behavior, Hyperstability, and Population Declines of an Aggregating Marine Fish

Descensos de Comportamiento, Hiperestabilidad y Población de Una Agregación de Peces Marinos

Baisses Comportement, Hyperstabilité, et la Population D'un Poisson Marin Agrégation

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EXTENDED ABSTRACT

Collapses of marine fish populations are a global concern. Some collapses are attributed to hyperstability, where catch per unit effort remains stable while the population declines. Hyperstability is difficult to detect until after a population is depleted, thus nearly all such studies on the hyperstability phenomenon are retrospective. Using whole-island acoustic arrays to track an endangered, aggregating reef fish on two Caribbean islands, we demonstrate for the first time behavioral mechanisms that might lead to hyperstability. We show that:

i) Every reproductive-aged fish aggregates each year,
ii) Older, more fecund fish aggregate longer,
iii) Individuals will visit multiple aggregation sites during the spawning period, yet every fish always aggregates and spawns at a single location, and
iv) Overfishing extends the time spent aggregating, increasing vulnerability to harvest as the population declines.

This latter finding is supported by historic accounts from other aggregation sites throughout the Caribbean. Taken together, our results demonstrate that aggregation sites are a surprisingly complete and persistent geographic bottleneck for aggregating species, and this bottleneck is a feature that intensifies with depletion. Our results highlight both the extreme vulnerability of local populations to harvest but the potential for even heavily harvested aggregations to recover.

Stock assessment often relies on proxies to estimate population size and set management targets. These proxies, such as catch-per-unit-effort (CPUE) rely on an assumed relationship between the proxy and the actual value of interest. In other words, the relationship between CPUE and stock size can be easily described and is often assumed to be linear; it is typically described by the equation CPUE = q x B, where “B” is biomass and “q” is “catchability”. For CPUE therefore, as a fish population (B) declines or increases, it becomes, respectively, harder or easier to catch a given unit of fish, but the relationship between how many fish they are and how hard they are to catch (q) is relatively constant (Figure 1). However, alternative relationships can exist, and under these scenarios, when expectation does not meet reality, a substantial decline in population size can occur before our abundance proxy detects the decline. Such a scenario was documented in the collapse of the Atlantic cod (*Gadus morhua*) fishery (Walters and Maguire 1996, Rose and Kulka 1999). When q increases as population size decreases (which stabilizes CPUE) the population is said to be hyper-stable (Hilborn and Walters 1992). In such instances, the assumption that CPUE is proportional to the population size will mask the population decline until the population has reached very low levels.

The majority of studies evaluating hyperstability have been retrospective (post-mortem) analyses based on evaluation of data to identify the causes of stock collapse (Walters and Maguire 1996, Rose and Kulka 1999, Erisman et al 2011). In these cases, hyperstability has been blamed on population density remaining constant while the population size and spatial distribution of the species declines. While previous research has developed a general idea of how hyperstability can manifest itself, no specific behavioral mechanisms have been identified.

Based on work conducted over the last 10 years through the REEF/Cayman Islands Grouper Moon Project, which focuses on the reproductive ecology of Nassau grouper (*Epinephelus striatus*) we identify specific behavioral mechanisms to describe how hyperstability can occur through activities associated with the species’ annual participation in large regional fish spawning aggregations (FSAs).

Through a combination of acoustic telemetry, conventional tagging, and direct observations of spawning behavior, we have discovered that:

i) All Nassau grouper aggregate every year (Semmens et al. 2005),

ii) Older (larger) fish aggregate for a longer period of time -- a 50 cm fish may spend 130 hours on the aggregation, while a 70 cm fish would spend 230 hours (Semmens et al. 2007, Semmens et al. unpublished data),
iii) Fish travel long distances during an aggregation, even if the FSA is not far from their home territory, with some fish swimming up to 230 km around an island < 20 km in length (Semmens et al., unpublished data), and
iv) Smaller aggregations aggregate for a longer period of time, with a 500-fish aggregation potentially occurring for as much as 125 hours (5 days) longer than a 3500 fish aggregation (Semmens et al., unpublished data)

Hyperstability has been defined as CPUE staying the same as abundance declines, essentially a "masking" effect on population trends, and has been attributed to fish continuing to pack themselves at the same density but the mechanisms for hyperstability to this point have been inferred. Here we provide behavioral evidence for how hyperstability manifests for aggregating species. Our data indicate that for aggregating species like Nassau grouper, hyperstability is not simply a density and distribution issue as has been previously described for other species, but rather a life history issue. Behaviorally-mediated vulnerability issues provide a potential mechanism for depensation (Allee effects) under the guise of hyperstability. Finally, based on these results we conclude that:

i) Protecting only some (but not all) regional FSAs will not protect fish from overexploitation, and
ii) Protecting only the FSAs themselves and not the corridors to and from the FSAs will not protect fish from overexploitation.

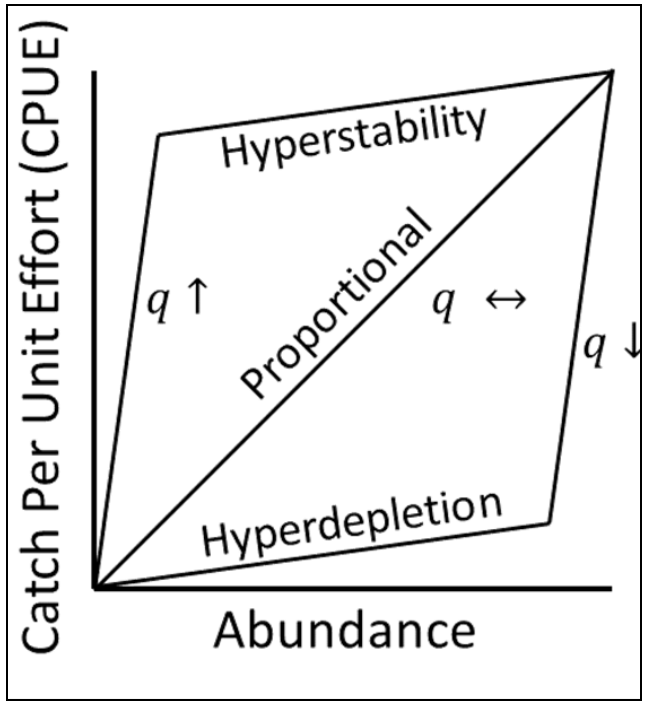

Figure 1. The relationship between true abundance and catch-per-unit effort. Under standard model assumptions, CPUE is assumed to be proportional to abundance. Hyper-stability occurs when catchability increases with decreasing stock size. Hyper-depletion, where q drops faster than the population and therefore results in an under-estimate of abundance, is shown for contrast.

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