Fish, jellyfish, and Killing the Winner

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Summary
Killing the Winner (KtW) is a generic model of competition involving a defense specialist and a competition specialist that is controlled by a predator. It has previously been proposed that this model might predict how mass is channelized between fish and jellyfish as a function eutrophication and water clarity in the Baltic Sea. The main finding from this approach is that above a certain eutrophication threshold, all added mass to the system will channel directly to jellyfish. Here we analyze observations from several areas where major jellyfish blooms have been reported. In systems where jellyfish have a relatively large footprint, like the Black Sea, our results suggests that the abundances of fish and jellyfish are consistent with the KtW predictions previously described for the Baltic Sea. However, in systems like the northern Benguela and the Bering Sea, jellyfish, although present in comparable biomasses to fish, appear to leave a relatively small footprint, consuming only a moderate part of the available mass in the system. Thus, these systems could be considered as dominated by fish, not jellies.

Introduction
It has been proposed, based on experimental and field evidence, that jellyfish (here understood as cnidaria and ctenophores) are efficient predators of early life stages of fish and that such predation, in combination with intensive fishing, may contrain fish recruitment. Further, the observed dietary overlap (i.e. non-gelatinous zooplankton prey) of pelagic fish and jellyfish led to the hypothesis that abundant jellyfish may outcompete pelagic fish. The result is for jellyfish to *functionally replace* pelagic fish. This hypothesis implicitly assumes that jellyfish are better competitors for zooplankton than pelagic fish.

An alternative hypothesis is that the zooplanktivorous fish is the most efficient competitor for zooplankton, but that their competitive superiority ceases with environmental change involving e.g. decreased water clarity.This mechanism (*Killing the Winner*) has previously been proposed for the relationship between jellyfish and zooplantivorous fish in the Baltic Sea (Haraldsson *et al.* 2012).

Here we seek to evaluate the *functional replacement hypothesis* for three ecosystems the Bering Sea, the Northern Benguela and the Black Sea, as well the *Killing the Winner hypothesis* for the Black Sea.

Materials and methods
By applying published data on time series of bulk biomass together with the mean individual weight of fish and jellyfish, (Table 1), we estimate and compare the total energy consumption by fish and jellies based on empirically derived respiration rates as a function of individual wet weight {Acuña et al. 2011). Also, published estimates of zooplankton biomass is used to stipulate trends in potential resource availability. For the black Sea, we also use a time-series of the Secchi depth as a proxy for eutrophication. The expectation of the coexist-

ence model of Haraldsson *et al* (2012) is that the jellyfish biomass should decrease linearly with increasing secchi depth, while the fishes should increase linearly.

Results

For the Bering Sea and the Northern Benguela, energy consumption from fish is overall higher than that from jellyfish (Figure 1A). To evaluate the potential effects of jellyfish on zooplankton and on pelagic fish, we performed simple linear regression analyses for the relationships *jellyfish~zooplankton* and *jellyfish~pelagic fish*, for the Bering Sea and the Black Sea (we have no time series for jellyfish in Northern Benguela). We found no statistically significant relationships for the two systems ($R^2 \sim 0$, p-value > 0.1). However, For the Black Sea we find a positive and negative linear relationship between secchi depth (water clarity), and fish ($R^2 = 0.75$, p-value < 0.05) and jellyfish ($R^2 = -0.41$, p-value < 0.05) biomass respectively (Figure 1B).

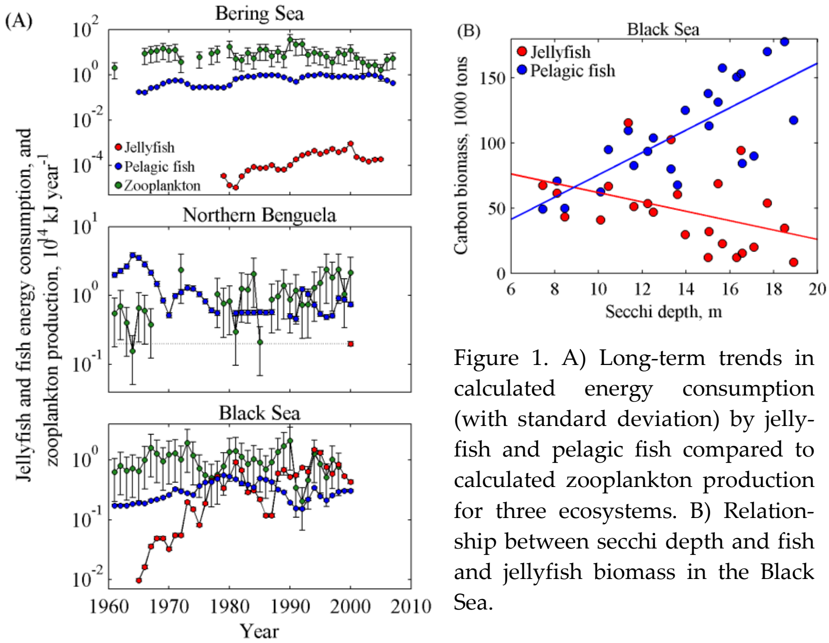

Figure 1. A) Long-term trends in calculated energy consumption (with standard deviation) by jellyfish and pelagic fish compared to calculated zooplankton production for three ecosystems. B) Relationship between secchi depth and fish and jellyfish biomass in the Black Sea.

Discussion

Trends of increasing jellyfish biomass, often several orders of magnitude, have been hypothesized to effect ecosystems, and pelagic fish in particular. However, energy requirements scales differently with biomass in pelagic fish and jellyfish (Acuña *et al.* 2011; Sørnes and Aksnes 2004). Biomass alone may therefore be insufficient to evaluate the impact of jellyfish on their surroundings. This might seem to be the case in the Bering Sea and the Northern Benguela I.e. it does not seem plausible that jellyfish have functionally replaces fish in these areas. For the Black Sea, where jellyfish biomass is reported several magnitudes greater than that of fish, their energetic requirements is comparable to that of pelagic fish. Here, a functional replacement scenario would be plausible. Our results also suggest that the biomass-relationship between fish and jellyfish are consistent with the KtW predictions previously described for the Baltic Sea (Haraldson *et al*. 2012).

References

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