



Synergies between climate anomalies and hydrological modifications facilitate estuarine biotic invasions

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Environmental perturbation, climate change and increasing international commerce are important drivers for biological invasions. Climate anomalies can further increase levels of habitat disturbance and, in principle, can act synergistically with these other drivers to elevate risk of invasion. Yet empirical evidence for climate extremes and their amplifying impacts in facilitating invasions is scarce. Coastal and estuarine ecosystems are especially susceptible to species invasion mediated by high inputs of non-indigenous propagules from ships' ballast water. A classic example of interaction between habitat modification and invasion of non-native species is the San Francisco Estuary, where accelerating rates of biotic invasions have been observed since the Gold Rush in 1849. This estuary has one of the longest, most complete estuarine zooplankton records available, starting in 1972, which allows identification of temporal patterns of species invasions and the most probable driving forces of invasions. Since the 1970s, the upper San Francisco Estuary has been invaded by eight exotic copepod species and two mysid species. Invasive zooplankton species did not become established until the 1970s when increasing propagule pressure from East Asia coincided with extended drought periods that were exacerbated by hydrological management. While this estuary experienced extended droughts in the past, hydrological changes associated with freshwater diversion since the mid-twentieth century increased the severity of drought and allowed unusually extreme salinity intrusions into the upper estuary. Drought periods since the mid-20th century would not have been as severe without anthropogenic hydrological perturbations, and salinity would have been within the historic range of salinity fluctuations. Anomalous drought conditions were the most likely stressors for native fauna not adapted to these unusual environmental conditions, and life history attributes of invasive zooplankton were advantageous enough during drought periods to outcompete native species and to colonize the system. This caused a major shift in zooplankton community composition and structure that affects energy transfer to higher trophic levels. Therefore, extreme climatic events, which may become more frequent under climate change, can act synergistically to facilitate the establishment of invasive species. These results have implications for biodiversity conservation and environmental management and suggest that estuarine ecosystem management needs to consider synergistic effects of extreme events with habitat perturbation when assessing invasion risks to coastal ecosystems.