

Invasive range expansion by the Humboldt squid, *Dosidicus gigas*, in the eastern North Pacific

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A unique 16-year time series of deep video surveys in Monterey Bay reveals that the Humboldt squid, *Dosidicus gigas*, has substantially expanded its perennial geographic range in the eastern North Pacific by invading the waters off central California. This sustained range expansion coincides with changes in climate-linked oceanographic conditions and a reduction in competing top predators. It is also coincident with a decline in the abundance of Pacific hake, the most important commercial groundfish species off western North America. Recognizing the interactive effects of multiple changes in the environment is an issue of growing concern in ocean conservation and sustainability research.

invasive species | top predators | top-down forcing

One of the greatest challenges in contemporary ocean science is that of predicting how oceanic communities will respond to impending changes, such as climatic warming and the removal of top predators (1). Interactive changes are of particular concern, but little information is available on the collateral effects of multiple factors. Rising temperatures have been implicated in shifting the geographical distribution patterns of fishes and plankton (2, 3) and in the disruption of plankton communities (4, 5). Removing top predators from an ecosystem can result in a cascade of effects that restructures the food web at lower trophic levels (6, 7) as well as at the top (8). Together, two or more such changes may act in ways that we cannot yet predict (9).

Here we demonstrate that the Humboldt squid, *Dosidicus gigas*, has greatly extended its perennial range in the eastern North Pacific Ocean. This geographic expansion occurred during a period of ocean-scale warming, regional cooling, and the decline of tuna and billfish populations throughout the Pacific (10). In this case, environmental changes off California are concurrent with invasion by a species from an adjacent region. Examples of invasion by species at higher trophic levels are relatively rare. The subsequent ecological impact of the Humboldt squid invasion can be seen in possible top-down forcing on the local population of Pacific hake, but the ecological effects may not yet be fully expressed (11). The question of how an oceanic community will respond to climatic change must include the possibility of invading species (12), and the consequences of removing top predators may depend on whether there is an ecological understudy waiting in the wings.

Dosidicus (Fig. 1) is a large, aggressive, abundant pelagic squid that reaches mantle lengths of 1.2 m, overall lengths >2 m, and weights up to 50 kg. Its geographical distribution is centered in the eastern equatorial Pacific. From these warm waters, its historical range extends along the subtropical coasts of both North and South America, with episodic but temporary range extensions to latitudes as high as 40° (13). Only a single species is known, although genetic evidence suggests that northern and southern populations are diverging (13, 14). *Dosidicus* feeds opportunistically on a broad range of pelagic and demersal fishes, crustaceans, and squids (15–17), many of which undertake vertical migrations of several hundred meters during a diel cycle (18). *Dosidicus* has a wide range in the vertical plane (19), encompassing that of its prey (Fig. 2). In turn, *Dosidicus* is preyed

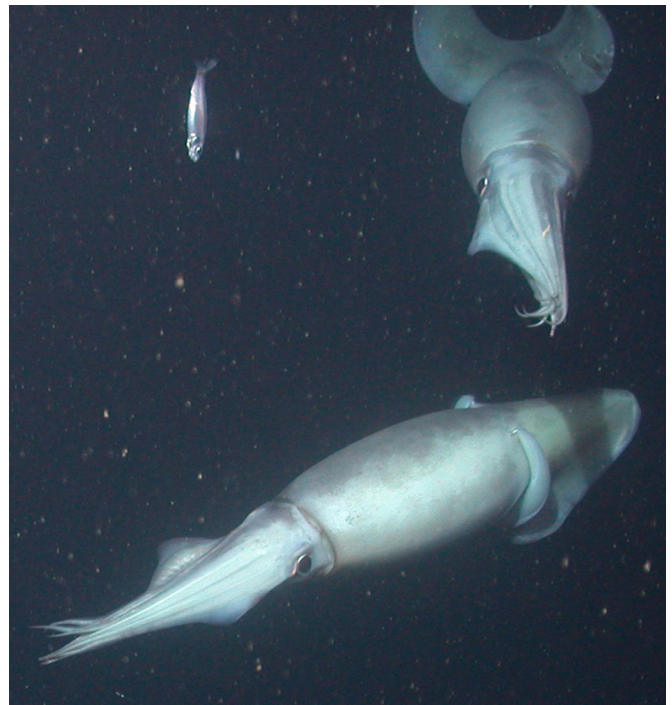


Fig. 1. Video frame grab of two *D. gigas*, observed at 524-m depth and 5.9°C, near the mode of the vertical distribution for the species in Monterey Bay. The fish is *Leuroglossus stilbius*, a deep-sea smelt ≈15 cm in length.

on by tuna, billfish, sharks, pinnipeds, and toothed whales (13, 17); it is also the specific target of commercial fisheries in Mexico, Peru, and northern Chile, where it is known as the jumbo squid, the jumbo flying squid, and jibia. Like other squids in the family Ommastrephidae, *Dosidicus* is believed to have only a 1- to 2-year life span (20), but its reproductive cycle, seasonality, and early life stages are still largely unknown, particularly outside the tropics. Short generation times have been shown to be advantageous in cases of warming-related range shifts (2) and also in response to changes in trophic structure (8).

Results

Our study is based on a unique data set of *in situ* video observations in deep water of the Monterey Submarine Canyon

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Abbreviation: ROV, remotely operated vehicle.

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only during warm El Niño periods. However, once it became established during the current cool regime, it has been present continuously. This demonstrates that, whereas *Dosidicus* may be associated with warm temperatures at the center of its distribution, it is physiologically adaptable and does not depend on the higher surface temperatures found in the tropics (19). There is no historical evidence to indicate that *Dosidicus* was a consistent part of the central California pelagic fauna during the previous (1950–1975) cool regime (22), which suggests that regime-shift oceanographic changes were not solely responsible for the present invasion.

In the eastern Pacific, the standing populations of tuna and billfish have recently experienced drastic depletions, effects felt not only in their abundance but also in their diversity (36, 37) and age structure (10). These large fishes are being replaced by smaller individuals, by smaller fish species, and by squid, a consequence also seen in other fisheries (8). *Dosidicus*, because it grows rapidly to large size and with no apparent seasonality to its reproduction (13, 38), can respond quickly to niches made accessible by the decline of large predatory fishes, which have longer life spans and delayed maturity (2, 8, 10). The removal of top predators like tuna and billfish may promote *Dosidicus* population growth and range expansion by reducing competition for their shared prey species. Likewise, it may reduce the mortality of juvenile *Dosidicus*, on which the large predatory fishes feed (13, 39).

The present situation off central California appears to be that a physiologically tolerant species (19) with a fast generation time has moved into a new area during a period of substantial climatic, oceanographic, and ecological changes. The occupation has lasted through multiple generations of the invading species (20),

which indicates a sustained population rather than a relict one or multiple invasions. The geographical range of the invader now extensively overlaps that of a large commercially valuable fish stock. If this trend continues, top-down forcing could have a major impact on the most abundant commercial groundfish population off the west coast of North America. A similar pattern may also be taking place in the Southern Hemisphere.

Materials and Methods

From 1989 to 1991, ROV-based video surveys covered the upper 500 m of the water column in Monterey Bay. In 1992, the vertical coverage was extended beyond 1,000 m. Quantitative video transects in a midwater time series occurred on about a monthly basis (21). These were supplemented by additional dives in Monterey Bay and offshore that supported other types of research. The total number of dives exceeds 3,000 over 16 years. As a result, this data set has greater temporal resolution than is the case for annual fishery-based catch statistics. Quantitative video surveys are much more useful for understanding holistic effects than are catch statistics alone, because they usually include both predators and prey, whereas traditional commercial sampling seldom enumerates both. Statistical analyses were performed by using SPSS 10.1 (SPSS, Chicago, IL).

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