

Part II

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## JUMBO SQUID (*DOSIDICUS GIGAS*) INVASIONS IN THE EASTERN PACIFIC OCEAN

Jumbo squid (*Dosidicus gigas*) are an important component of the marine ecosystem and a key target of marine fisheries throughout the Eastern Tropical Pacific (ETP), from the coast of Peru to the Gulf of California. Further north, in the California Current system (CCS), a reappearance of this species off Monterey after the 1997–98 El Niño resulted in an unusual persistence of the new population. Since 2003, jumbo squid have been regularly encountered in large numbers throughout the CCS and as far north as southeast Alaska. Likewise, jumbo squid have recently expanded the southern extent of their range from their traditional distribution along the waters off Peru to the central Chilean coast. In both hemispheres, invasions have been documented throughout the past century, as far back as the 1830s in Chile (Alarcón-Muñoz et al., this volume), however the spatial and temporal extent of the ongoing invasions appear to be unprecedented in the historical record.

Rapidly developing fisheries have landed up to several hundred thousand tons of squid per year in central Chile since 2003, where historical abundance and catches were previously minimal. As a result of this recent increase, and with the continued development of Peruvian, Mexican and high seas fisheries, commercial catches of jumbo squid are now greater than those for any other cephalopod in the world. In 2004 and 2005, nearly 800,000 tons a year were landed, while global annual landings prior to 2000 were never greater than 200,000 tons. Consequently, both the proximate causes of the ongoing range expansion, and the real or potential consequences of the range expansion to marine ecosystems and fisheries, are of major interest to researchers, resource managers and stakeholders throughout the Eastern Pacific Rim. The 2007 Symposium brought together biologists engaged in jumbo squid research from Chile to Canada to address many of these questions; these proceedings represent a substantial subset of that work.

Despite the increasing research efforts into jumbo squid biology, ecology and fisheries, the primary drivers of these range expansions remain uncertain. Climate-related mechanisms appear to be the most plausible, although the remarkable tolerance of adult squid to a wide range of environmental conditions suggests that the effects of climate change are likely to be far more complex than temperature alone. Rodhouse (this volume) provides a comprehensive review of the interactions between climate and ommastrephid squid populations, demonstrating the highly variable boom-and-bust cycles of commercially and ecologically important stocks throughout the Pacific and Atlantic Oceans. In most examples, changes in physical oceanic conditions appear to have played the most significant role, although the potential role of fishing on marine communities has often been invoked as an alternative, or complementary factor (Caddy and Rodhouse 1998; Zeidberg and Robison 2007). Climate change has already been shown to force the range expansions of many marine species towards the poles (Field et al. 2006), with animals with the highest turnover rates showing the most rapid distributional responses to warming (Perry et al. 2005). Jumbo squid would represent an extreme with respect to growth, turnover and adaptability; with the capacity to grow more than 2 mm per day, to nearly 2 m total length in just a little more than a year (Mejía-Rebollo et al., this volume). While the thermal tolerance of jumbo squid might discredit the idea of warming alone as being responsible for range variability and expansion (Gilly et al. 2006), a more subtle climate-related mechanism is certainly plausible.

For example, evidence continues to demonstrate an ongoing expansion of the oxygen minimum zone (OMZ) throughout the ETP, the CCS, and the North Pacific Ocean (Whitney et al. 2007; Bograd et al. 2008; Stramma et al. 2008; Vetter et al. this volume), and projections of

future climate suggest that this response is to be expected under most global change scenarios. A relatively shallow OMZ is a characteristic feature of eastern Pacific ecosystems, particularly in the southeast Pacific Ocean. This reflects the consequences of high levels of upwelling-driven primary production, much of which is metabolized by microbes leading to a vast region of low-oxygen water ranging between 100 to 1000 meters depth (Helly and Levin, 2004). This low-oxygen region provides a refuge for mesopelagic fishes and other organisms from surface-oriented visual predators. Interestingly, jumbo squid have shown a remarkable tolerance for these conditions (Gilly et al. 2006), and are a key predator of mesopelagic organisms in the ETP. In fact, their distribution seems to be linked with the distribution of low oxygen waters in the mesopelagic environment throughout the northeast Pacific Ocean (Gilly and Markaida 2007), suggesting that the ongoing intensification of the OMZ could represent an expansion of favorable habitat.

Potential consequences of these range expansions are difficult to evaluate and quantify. Jumbo squid primarily consume vast quantities of small, mesopelagic organisms, particularly myctophid fishes, in the core of their range (Nigmatullin et al. 2001; Markaida 2006). However, at the periphery in both hemispheres, jumbo squid also forage on commercially and ecologically important fish and invertebrates (Arancibia et al. 2007; Field et al. 2007), including commercially valuable groundfish such as hake (*Merluccius* spp.) and rockfish (*Sebastes* spp.). Yet jumbo squid are also a key forage item for many higher trophic level fishes and marine mammals throughout their range, particularly sperm whales (*Physeter macrocephalus*) and other toothed whales, as well as commercially important tunas, billfish and sharks (Clarke 1976; Olson and Watters 2003; Markaida and Hochberg 2005). The relative contribution of jumbo squid as prey to higher trophic levels can also be tremendous, as emphasized by their relative importance in shortfin mako shark (*Isurus oxyrinchus*) diets off of southern California. Although jumbo squid were rarely encountered in these waters prior to 2002, they comprise 30% to 40% of the diet (by volume) of mako sharks between 2002 and 2006 (Vetter et al., this volume). Similarly, abundance of these key prey items is contemplated as a potential factor in an apparent doubling of the abundance of sperm whales in the California Current over recent years (Barlow and Forney 2007). Consequently, these animals play a major role in structuring the pelagic and mesopelagic ecosystems throughout their range, with a potential mix of both positive and negative impacts to fisheries and fishing communities.

Disentangling the interacting effects of climate, fishing and other ecosystem changes pose considerable challenges in regions where the jumbo squid invasions have taken place. For example, as jumbo squid have become

more abundant off of central Chile, the range expansion has been linked with a decline in a key target of Chilean groundfish fisheries, Chilean hake (*Merluccius gayi*). Yet the significance of the contribution of jumbo squid to the decline in hake relative to that of fishing remains the subject of ongoing debate. In fact, Arancibia and Neira (this volume) suggest that the greatest decline in Chilean hake populations took place during a period of high fishing mortality, prior to the onset of high abundance of squid. Their evaluation of the relative impacts of fishing and predation with dynamic ecosystem models indicates that squid predation was negligible relative to the impacts of fisheries and cannibalism. Alternatively, Alarcón-Muñoz et al. (this volume) present an interpretation in which at least part of the decline of hake is attributable to squid. Additionally, as Holmes et al. (this volume) illustrate, the impacts of jumbo squid on fisheries could possibly be more subtle than direct predation alone. Holmes et al. argue that the presence of jumbo squid during hydroacoustic surveys of Pacific hake in the California Current may lead to major changes in hake schooling behavior. Biological consequences of altered schooling behavior are not clear, but impacts on foraging, migrating or spawning would probably be deleterious to a local population. Additionally, altered schooling may confound the ability to monitor, assess, and possibly manage this important commercial resource.

Although there is a growing body of knowledge regarding both the potential causes and likely consequences of jumbo squid invasions, fully understanding the cumulative impacts on marine ecosystems will be difficult. As Markaida et al. (this volume) discuss, jumbo squid appear to show remarkable plasticity in foraging behavior, with a high dependence on mesopelagic micronekton throughout most of their range, coupled with unpredictable horizontal movements that may represent explorations for improved, and opportunistic, foraging grounds. These authors suggest that the balance between stable and opportunistic foraging may be critical in determining how long jumbo squid will remain in a given area, an insight that may prove useful in evaluating the likelihood as well as the consequences of future movement patterns. Similarly, Keyl et al. (this volume) demonstrate that jumbo squid exhibit tremendous plasticity in their rates of growth, maturity and likely survival; key factors that facilitate adaptation to a growing range of marine environments and ecosystems.

All of these points illustrate the tremendous need for a basic science assessment of the life history, distribution and habitat associations, abundance, and ecological impacts of jumbo squid throughout their range. The 2007 Symposium on jumbo squid invasions included eight invited papers, another nine contributed papers, and eight

posters from researchers based in at least seven countries. This reflects the widespread and ongoing efforts throughout the eastern Pacific Ocean to improve our understanding of the life history, distribution, behavior and ecological interactions of these important animals. The articles presented here were refereed by at least two external reviewers and edited by John Heine and Sarah Shoffler, all of whom deserve considerable thanks and credit for their efforts. Additional thanks go to the many symposium presenters and participants, as well as Anne Allen and other SWFSC staff for assisting with logistics. Tremendous thanks are given to the Symposium sponsors, including the Sportfishing Association of California, the California Wetfish Producers Association, the Pacific Marine Conservation Council and the Hubbs SeaWorld Research Institute, whose support was particularly helpful in facilitating widespread international participation.

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