Deep-Sea Research II 95 (2013) 197–208

Contents lists available at ScienceDirect

Deep-Sea Research II

journal homepage: www.elsevier.com/locate/dsr2

Behavioral ecology of jumbo squid (*Dosidicus gigas*) in relation to oxygen minimum zones

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ARTICLE INFO

Available online 28 June 2012

Keywords:
Deep scattering layer
Diel vertical migration
Diet
Diving
Humboldt squid
Hypoxia
Oxygen minimum zone
Range expansion
Satellite tagging

ABSTRACT

Habitat utilization, behavior and food habits of the jumbo or Humboldt squid, *Dosidicus gigas*, were compared between an area recently inhabited in the northern California Current System (CCS) and a historically established area of residence in the Gulf of California (GOC). Low dissolved oxygen concentrations at midwater depths define the oxygen minimum zone (OMZ), an important environmental feature in both areas. We analyzed vertical diving behavior and diet of *D. gigas* and hydrographic properties of the water column to ascertain the extent to which squid utilized the OMZ in the two areas. The upper boundary of the OMZ has been shoaling in recent decades in the CCS, and this phenomenon has been proposed to vertically compress the pelagic environment inhabited by aerobic predators. A shoaling OMZ will also bring mesopelagic communities into a depth range with more illumination during daytime, making these organisms more vulnerable to predation by visual predators (i.e. jumbo squid). Because the OMZ in the GOC is considerably shallower than in the CCS, our study provides insight into the behavioral plasticity of jumbo squid and how they may respond to a shoaling OMZ in the CCS. We propose that shoaling OMZs are likely to be favorable to jumbo squid and could be a key indirect factor behind the recent range expansion of this highly migratory predator.

1. Introduction

During the last decade jumbo squid (also called Humboldt squid, *Dosidicus gigas*) have been undergoing a major range expansion in the eastern Pacific Ocean, where they are endemic. This species generally inhabits areas beyond the continental shelf but is well known for transient excursions into shallower coastal waters that often result in mass strandings. Jumbo squid are large, highly migratory, and effective visual predators capable of tolerating large and rapid changes in environmental conditions, including pressure, temperature and dissolved oxygen concentration (Gilly et al., 2006). Understanding the behavior of such predators and their ecosystem interactions, particularly in conjunction with climate change, has been of great interest to ecologists, fisheries scientists and commercial fishing operators. Studies concerning horizontal movements and diet have occurred in the northern California Current System (CCS) during this range expansion (Field et al., 2007, 2013; Zeidberg and Robison, 2007) as well as in the central Gulf of California (GOC) (Gilly et al., 2006; Markaida and Sosa-Nishizaki, 2003; Markaida et al., 2005, 2008), where jumbo squid have occurred in commercial quantity year-round since the mid 1990s (Markaida et al., 2005) except several years associated with El Niño events (Gilly and Markaida, 2010; Markaida, 2006).

Pop-up archival transmitting (PAT) satellite tags have been successfully deployed and recovered in the assessment of relatively short-term (< 1 month) patterns of vertical movement and habitat use of jumbo squid in the GOC (Gilly et al., 2006) and the Pacific coast of Baja California (Bazzino et al., 2010). These studies have revealed general patterns in vertical migration. Daytime is typically spent in the midwater environment with shallower depths occupied at nighttime, but rapid migrations throughout the water column can occur at any time.

In the eastern tropical Pacific (Nigmatullin et al., 2001), as well as in the northern CCS (Field et al., 2007, 2013), the GOC (Markaida and Sosa-Nishizaki, 2003) and off the Pacific coast of Baja California (Bazzino et al., 2010), jumbo squid feed primarily on small mesopelagic fishes, squids, and crustaceans that are components of the acoustic deep scattering layer (DSL). However, in the northern CCS, significant predation also occurs on a variety of much larger fishes of considerable ecological and commercial importance, including Pacific hake (*Merluccius productus*), several species of rockfish (*Sebastes* spp.), many flatfish species (Pleuronectidae) (Field et al., 2007) and even salmonids (Braid et al., 2012; Field et al., 2013).

The eastern Pacific Ocean is characterized by the world's largest and shallowest oxygen minimum zone (OMZ) (Keeling et al., 2010), a midwater region where the dissolved oxygen (DO)

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0967-0645/$ - see front matter © 2012 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.dsr2.2012.06.005

concentration is ≤20 μmol/kg, or ~0.5 mL/L (Fig. 1; Helly and Levin, 2004). Several recent studies have indicated an ongoing expansion of the OMZ, primarily through shoaling, throughout the eastern Pacific (Bograd et al., 2008, 2010; Stramma et al., 2008; Whitney et al., 2007), and scenarios of the climate change suggest a continuation of this trend in the future (Deutsch et al., 2011; Keeling et al., 2010).

Shoaling of midwater hypoxic regions in the Atlantic Ocean has been shown to cause vertical habitat compression of the well oxygenated, upper water column inhabited by predatory fishes and may result in an increased susceptibility to commercial fishing pressure (Prince and Goodyear, 2006; Prince et al., 2010; Stramma et al., 2011). Although DO in these regions is considerably higher than that in the Pacific OMZ, the effects of a shoaling hypoxic front are likely to be similar in both areas. Another potential effect of a shoaling OMZ in the Pacific is the translocation of mesopelagic communities that inhabit the upper OMZ to shallower, more illuminated depths, and this could make these mesopelagic organisms more susceptible to visual predators (Koslow et al., 2011).

Clearly there are multiple and interacting effects expected for pelagic predators in association with OMZ shoaling, and not all predators are likely to be affected in the same ways. Jumbo squid forage largely on the mesopelagic micronekton that comprise the DSL, and because they are visual predators that can tolerate cold, low oxygen conditions (Gilly et al., 2006), they might be favored relative to other pelagic predators by a shoaling OMZ.

This study provides insight concerning the question of how a shoaling OMZ may affect jumbo squid, a highly migratory predator. We tagged large squid off central California in the CCS and analyzed their diving behavior and vertical habitat use in relation to the OMZ (≤20 μmol/kg DO) and the hypoxic region above it (20–60 μmol/kg DO). Because models predict a continued shoaling of the OMZ in this region, we reanalyzed existing jumbo squid tag data from the Guaymas Basin in the GOC, a region where the OMZ is much shallower and perhaps similar to the future scenario for the CCS. In both regions, we also compared new and existing food habits data to infer differences in foraging behavior. *Dosidicus gigas* is a species that clearly utilizes the upper OMZ in the GOC and likely uses this environmental feature in conjunction with both foraging on mesopelagic organisms and predator avoidance (Davis et al., 2007; Gilly et al., 2006). This is also the case in the northern CCS, but squid in this region utilize the continental shelf environment to a much greater extent. We find that jumbo squid can tolerate cold, hypoxic conditions for long periods, perhaps longer than most, if not all, large pelagic competitors and predators. They can also make rapid deep dives across the OMZ to depths of >1200 m, probably as an escape mechanism from some of those predators. Shoaling of the upper OMZ could thus uniquely favor jumbo squid, and we propose that this changing midwater feature is an important indirect factor behind the recent range expansion of this species in the northern hemisphere.

2. Methods

2.1. Vertical habitat and behavior

2.1.1. Tagging

All squid in this study were collected with weighted luminescent jigs (0.35 m) using rod and reel or hand-line, carefully brought onboard the vessel by lifting the jig with a heavy monofilament leader, and tagged on the ventral side of the fin as close to the gladius as possible with Mk10 pop-up archival transmitting tags (PAT: Wildlife Computers, Redmond, Washington, USA). Previously described tagging procedures (Gilly et al., 2006) were modified in 2006, mainly by securing the tag to a small plastic platform (from which it released) that was attached to the squid's fin by two nylon bolts (1/4-20) and secured with nylon washers and nuts. Squid in the CCS were tagged in autumn (2008–2009), and squid in the GOC were tagged in the Guaymas Basin during spring and autumn (2004–2008). Tags were programmed to record temperature (resolution of 0.05 °C) and pressure (depth resolution of 0.5 m) at 1 Hz, and a full record of archived data was available upon recovery of the tag. CCS tags in 2009 were able to upload a 0.01 Hz subsampled record to Argos,

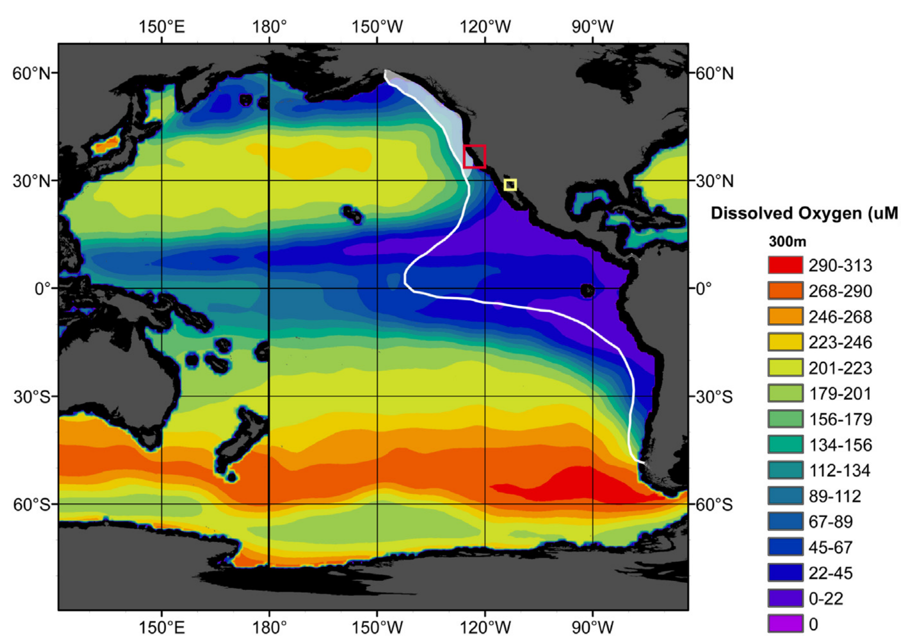

Fig. 1. Dissolved oxygen at 300 m in the Pacific Ocean with the approximate range of jumbo squid (white curve). The recent range expansion at the northern limit is shown shaded in transparent white. Dissolved oxygen data and map are from the World Ocean Atlas Database (www.nodc.noaa.gov/OC5/WOA01F/prwoa01f.html). Focus regions in this study are boxed: the CCS in red and the GOC in yellow. Detailed maps of tagging locations are published elsewhere (Stewart et al., in review; Gilly et al., 2006; in press).