

LARGE-SCALE RANGE EXPANSION AND VARIABILITY IN OMMASTREPHID SQUID POPULATIONS: A REVIEW OF ENVIRONMENTAL LINKS

PAUL G. RODHOUSE

British Antarctic Survey
Natural Environment Research Council
High Cross, Madingley Road
Cambridge CB3 0ET, UK
p.rodhouse@bas.ac.uk

ABSTRACT

Over the last four decades, several ommastrephid squid stocks have shown rapid expansion and contraction, driving highly variable and sometimes boom and bust fisheries. These include *Illex illecebrosus* in the northwest Atlantic Ocean, *I. argentinus* in the southwest Atlantic Ocean, *Todarodes pacificus* in the northwest Pacific Ocean, *T. sagittatus* in the Norwegian fjords, and *Dosidicus gigas* in the Peru and California Current systems. Explanations for the highly variable behavior of squid populations include: (1) direct effects of environmental variability; (2) changes in prey availability, especially for the early life stages; (3) changes in predation, disease and parasitism; and (4) exploitation of predatory fish which might reduce predation pressure and thus create vacant niches into which the short-lived, ecologically opportunistic squid can expand. This review focuses on the effects of environmental variability on populations and possible interactions with fisheries. Apart from *Dosidicus gigas*, which is associated with the coastal upwelling systems of the Pacific Ocean's eastern boundary currents, the ommastrephid fisheries are mostly pursued in the high energy, western boundary current systems. The environmental variability that will drive changes in population size will differ between these environments. The recent range expansion of *Dosidicus gigas* in the Eastern Pacific Ocean seems to have increased predation pressure on hake stocks off North and South America, which may affect fisheries. The El Niño/Southern Oscillation event in the Pacific Ocean is a well-documented, highly variable oceanographic event and the fisheries along the western seaboard of North and South America are also among the best documented. The *Dosidicus gigas* range expansion over the last decade may provide an opportunity to explore the interacting effects on a squid population of environmental variability and ecological change caused by fishing.

INTRODUCTION

Invasions and range expansions of cephalopod populations have been known to scientists for the best part of at least two hundred years, and may even explain the origin of the late Minoan octopus culture of the eastern

Mediterranean Sea around the 15th century B.C., in which images of octopus were used to decorate earthenware from pots and vases to coffins. There are certainly more recent historical records of octopus invasions in the English Channel that caused substantial damage to shellfish fisheries at the turn of the 20th century and again in the 1950s (Garstang 1900; Rees and Lumby 1954).

In the Eastern Pacific Ocean, D'Orbigny (1835–43) describes large strandings of *Dosidicus gigas* on the Chilean coast in the early 19th century, and there are also reports of the species being very abundant off the west coasts of North and South America in the 1930s (Clark and Phillips 1936; Gunther 1936; Croker 1937). Over the last decade, and since the major 1997 El Niño/Southern Oscillation (ENSO) event, there has been a large-scale range expansion of *Dosidicus gigas* northwards as far as Alaska and southwards to southern Chile (Field et al. 2007; Zeidberg and Robison 2007). The cause of this expansion is debated, and ranges from the relative importance of life history response to thermal change and the possible effects of the reduction of tuna stocks from overfishing (e.g., Watters et al. 2008; Zeidberg and Robison 2008). Compounding this debate are the changes in the structure of the pelagic community off both North and South America. Holmes et al. (2008) suggest that the range expansion of *Dosidicus gigas* has increased predation pressure of squid on hake stocks off North and South America, which may have caused changes in hake behavior. This may also have implications for the hake fisheries (Arancibia and Neira 2008).

Elsewhere, fishery data records have quantified the magnitude of variability of population size of exploited cephalopod species, especially of the family ommastrephidae. The longest record exists for the Japanese *Todarodes pacificus* fishery in the Kuroshio/Oyashio current system, for which data go back to the beginning of the 20th century. These data indicate that the population size varied on both an annual and a decadal basis, with higher catches during warm phases in the decadal record of the local climate regime (Sakurai et al. 2000) (fig. 1). A shorter data set exists for *Illex argentinus* in the southwest Atlantic Falkland/Brazil Current system, where the catches varied interannually by over an order of mag-

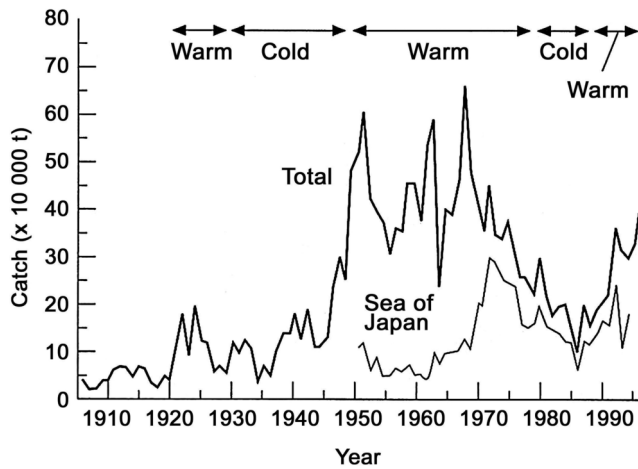


Figure 1. Annual variability in the total Japanese catch of *Todarodes pacificus* in the northwest Pacific Ocean and in the Sea of Japan (source: Sakurai et al. 2000).

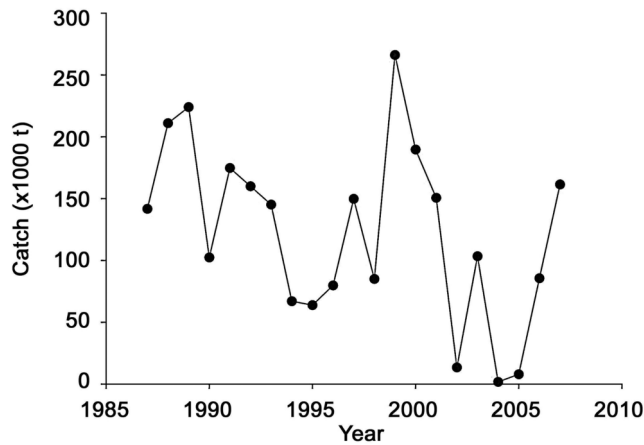


Figure 2. Annual variability in the catch of *Illex argentinus* in the Falkland Islands fishery, southwest Atlantic Ocean (source: Falkland Islands Government Fisheries Department Statistics, Stanley, Falkland Islands).

nitude in two decades (fig. 2). Similarly, a short-term data set for *I. illecebrosus* in the northwest Atlantic Gulf Stream/Labrador Current system illustrates the short boom-and-bust cycle of that fishery in the decade 1973–83 (fig. 3). The Peruvian fishery for *Dosidicus gigas* has been very well documented since the inception of an industrial fishery in the early 1990s; the record includes the period of the extreme ENSO event of 1997–98 and shows a dramatic variability in abundance since the beginning of the record (fig. 4).

These fisheries all use lights and jigs and are visible in Defense Meteorological Satellite Program (DMSP) imagery (Rodhouse et al. 2001). These images have been used to follow the spatial dynamics of the fisheries (Kiyofuji and Saitoh 2004; Waluda et al. 2002; 2004; 2005), and in a recent paper, Waluda et al. (2008) related interannual changes in catch of *Illex argentinus* to changes in the distribution of the fishing fleet.

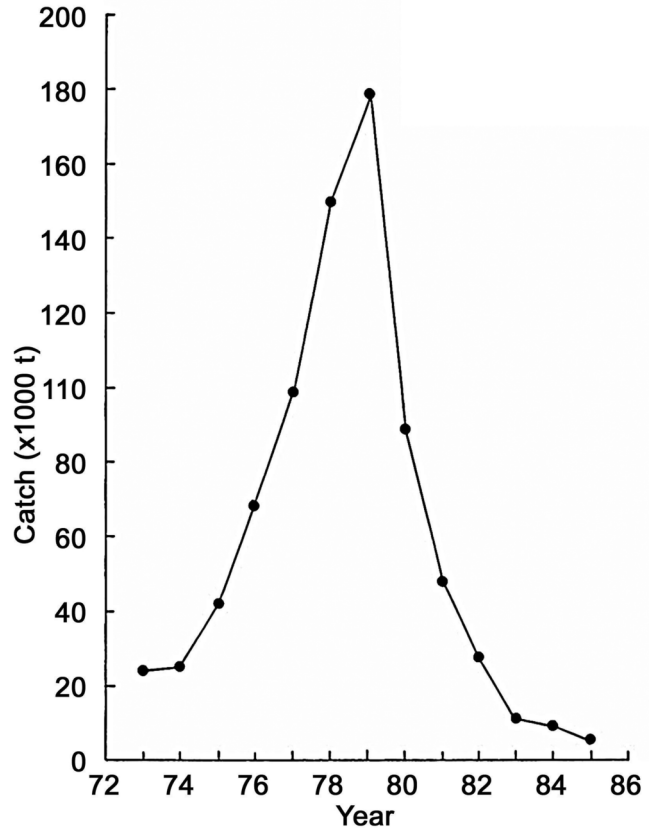


Figure 3. Annual variability in the catch of *Illex illecebrosus* in the northwest Atlantic Ocean (source: FAO Fishery Statistics, FAO, Rome).

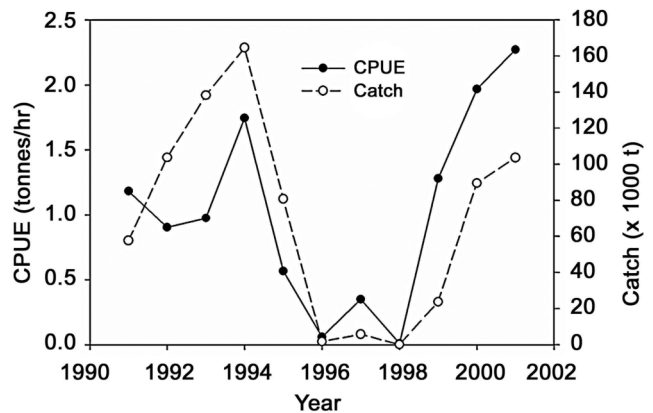


Figure 4. Annual variability in catch and catch per unit effort (CPUE) for jumbo squid, *Dosidicus gigas*, in Peruvian waters (source: Instituto de Mar del Perú, IMARPE, Callao, Peru).

The purpose of this paper is to review the theoretical causes of variability in size and range of ommastrephid squid populations and to examine the data in order to test some of the theoretical causes. Given the scale of the processes involved, data from the commercial fisheries provide insight into population processes and remotely sensed oceanographic data provide a better understanding of the environmental processes. The possible interaction of fishery effects on the ecosystems inhabited by

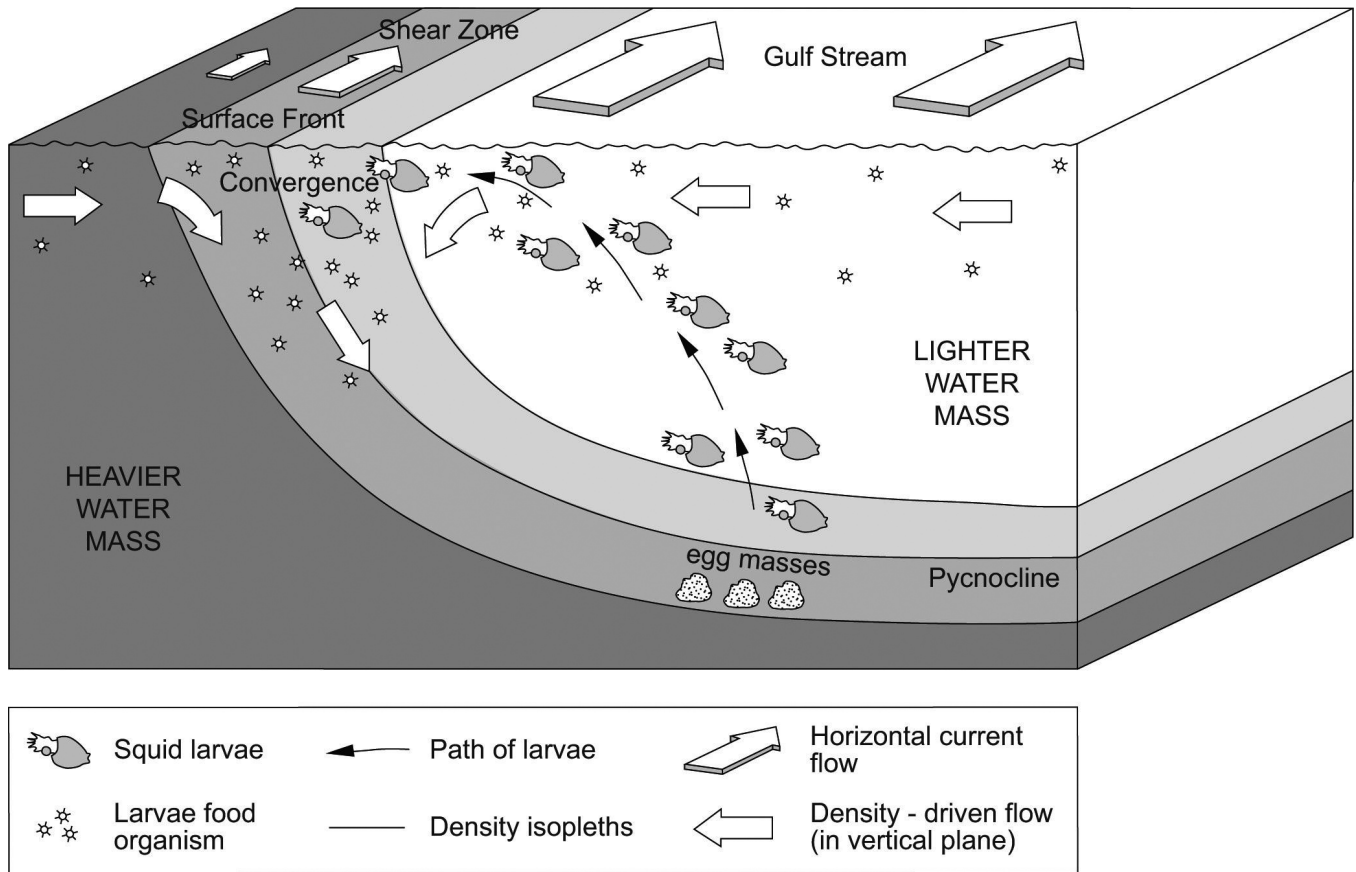


Figure 5. Schematic diagram showing the relationship between the early life cycle of an ommastrephid squid and the physical oceanographic processes at the convergent frontal zone between the waters of a western boundary current (e.g., the Gulf Stream) and adjacent shelf slope water (source: Bakun and Csirke 1998).

ommatrephid squid and environmental variability is also considered, as this may be one of the multiple causes of variability and change in these squid populations.

BIOPHYSICAL INTERACTIONS— THEORETICAL CONSIDERATIONS

The body of theory that explains and predicts variability in cephalopod populations in relation to fisheries has largely focused on interactions between biological processes, especially in the early life stages of eggs and paralarvae, and physical oceanographic variability.

Western-boundary current systems

Most of the large fisheries for ommastrephid squid occur in the western-boundary current systems of the northwest Pacific Ocean (*Todarodes pacificus*), the southwest Atlantic Ocean (*Illex argentinus*), the northwest Atlantic Ocean (*Illex illecebrosus*), and the southwest Pacific Ocean (*Nototodarus gouldi* and *N. sloanii*). These currents are powerful, meandering systems that generate warm- and cold-core rings and provide “rapid transport” systems for planktonic squid eggs and larvae.

Understandably, in view of the importance of fish-

eries in these systems, most theory and data on the interactions between squid populations and physical oceanography have been focused on the stocks inhabiting western-boundary current environments. The ommastrephid life cycle in these systems is generally well known (Okutani 1983; Haimovici 1998; O’Dor and Dawe 1998). The squid have a one-year life span and spawn in low-latitude warm water. The planktonic eggs and larvae develop in this environment and are subject to transport by ocean currents. When the juvenile squid have grown into the nektonic phase, some, or all, of the young population migrates in the direction of the prevailing flow into cooler, higher latitude waters where productivity is higher, food is more abundant, growth is faster, maximum size is larger, and hence, fecundity is maximized (O’Dor and Coelho 1993).

A theoretical framework for recruitment variability in western-boundary current ommastrephid squid populations has been set out by Bakun and Csirke (1998). They identify the habitat requirements for squid reproduction to be: (1) food web enrichment by physical processes, e.g., upwelling; (2) a mechanism for formation of concentrated patches of food such as convergent

flow patterns and frontal systems; and (3) flow mechanisms that allow the population to maintain itself. Bakun and Csirke (1998) propose that western boundary currents meet these habitat requirements (fig 5).

Fast-flowing geostrophic currents, for example, the Gulf Stream and the Brazil and Kuroshio Currents, occur at the interface of waters of different density (i.e., shelf/slope waters and offshore waters of the oceanic gyre) where baroclinic pressure balances Coriolis accelerations generated in high-speed ocean currents. When the two water masses of different density and relative motion come together, dynamic forces generate flow convergence towards the intersection and friction in the shear zone perturbs geostrophic balance. Gravity and pressure cause the denser shelf/slope water to sink below the less dense oceanic water, which then overflows the shelf/slope water. Mixing at the interface produces water of intermediate density which flows below the surface water. Both the high- and low-density water masses thus form a mass of mixed water that sinks at the interface. The buoyancy-driven flows that supply the formation of this mixed water are directed from each water mass towards the interface, resulting in a convergence zone that sustains the frontal boundary.

Bakun and Csirke (1998) describe these processes: these processes form a pycnocline (see fig. 5) where ommastrephid egg balloons are neutrally buoyant at a depth where there are suitable temperatures and low predation. The hatching paralarvae rise to the surface and are carried to the convergent frontal zone by the density-driven flow described above. In the frontal zone, eddy formation drives upwelling of nutrient-rich water which enriches the food chain. Furthermore, convergence at the surface front and in its meanders concentrates the food resource.

In addition to the above processes, western-boundary current systems potentially provide rapid transport of eggs and paralarvae from the spawning ground to the feeding ground. However, this might be reduced in the frontal shear zone between the boundary current and shelf water, and the distance carried will be increased in meanders that will lengthen the trajectory. Warm-core eddies will carry eggs and paralarvae onto the continental shelf providing a positive advantage. Conversely, cold-core eddies will carry eggs and paralarvae into the ocean interior where they will be lost from the population.

Hypotheses concerning recruitment variability in relation to physical oceanographic variability assume that favorable conditions exist when: (1) the surface frontal zone maintains its integrity and there is a low frequency of core ring formation; (2) eggs and paralarvae are transported from the oceanic gyre to the shelf adult feeding grounds; (3) food availability and low predation favor adult counter migration; (4) paralarva hatch when in the

presence of food; and (5) there are low levels of predation, disease, and parasitism throughout the life cycle.

Eastern-boundary current systems

Large populations of *Dosidicus gigas* inhabit the eastern-boundary current systems of the eastern Pacific Ocean and support important fisheries in the Peru Current upwelling system in the southeast Pacific Ocean and in the Gulf of California. Eastern-boundary currents provide a different environment to western-boundary currents; they are weak and characterized by regions of major coastal upwelling that support high primary productivity which, in turn, provides squid populations with enriched feeding conditions. The theory concerning which factors drive recruitment variability is less well developed for the eastern-boundary current systems. However, the interactions between ENSO events and production processes in the eastern Pacific coastal upwelling systems are well known and appear to play a major part in driving variability in *Dosidicus gigas* recruitment and population size (Waluda et al. 2006; Yamashiro et al. In prep.). By relaxing the flow of surface water from the coast into the interior of the Pacific Ocean, ENSO events may favor retention of eggs and paralarvae in the nearshore regions where the fishery is pursued (Anderson and Rodhouse 2001). Conversely, during normal conditions and cold (La Niña) events, offshore transport of surface water may cause entrainment of eggs and paralarvae towards the central Pacific Ocean so that they are dispersed and the cohort develops over a larger area at a lower density.

BIOPHYSICAL INTERACTIONS— OBSERVATIONAL DATA

Western-boundary current systems

The influence of environmental variability on ommastrephid squid population size and extent has been analyzed using Japanese catch data and paralarval densities for *Todarodes pacificus* together with remotely sensed sea surface temperature (SST) data (Sakurai et al. 2000). Egg and paralarvae data suggest that the spawning grounds occur over the continental shelf at sea surface temperatures between 15°–23°C. Using SST data analyzed with GIS technology, it was shown that since the late 1980s, winter spawning areas over the continental shelf and slope in the East China Sea (defined by 15°–23°C) have expanded over the distribution range of the population and separate autumn and winter spawning areas have coalesced. This has been coincident with increases in abundance reflected by catch rates (catch per unit effort or CPUE) of adult *T. pacificus* (fig. 1) and paralarval densities. The conclusion to be drawn here is that as the available thermal habitat suitable for spawning and egg and

paralarval survival increases, the population has responded positively and population size has increased.

In the southwest Atlantic Ocean, a similar approach combining data from the *Illex argentinus* fishery and remotely-sensed SST data was taken (Waluda et al. 1999). An analysis of SST on the spawning grounds around the Patagonian shelf edge at 35°S and CPUE in the Falkland Island fishery the following fishing season—when the progeny from the spawning ground would be exploited—was carried out over a thirteen-year period. It was found that adult abundance was influenced by SST on the spawning grounds in the winter spawning season prior to the fishery. The relationship was negative and SST on the spawning grounds explained about 45% of the variability in population size over the time covered by the study. Time-series analysis revealed that there were connections between SST in the south Atlantic Ocean and ENSO events in the tropical Pacific Ocean, with a two-and-a-half year lag between the Pacific Ocean and the southern Patagonian shelf (where the fishery is pursued), and a five-year lag between the Pacific Ocean and the northern Patagonian shelf (where the spawning grounds are located). This suggests that population variability in the *Illex argentinus* population in the south Atlantic Ocean is ultimately driven by ENSO events in the Pacific Ocean.

In a further study, Waluda et al. (2001) examined the possible influence of mesoscale oceanographic variability in the spawning area on subsequent recruitment success in the *Illex argentinus* fishery. The study had two parts: the first examined the relationship between recruitment in the Falkland Islands fishery and the integrity of the confluence front in the spawning area around the Patagonian shelf edge at 35°S; and the second part examined the relationship between recruitment and the proportion of the spawning area in which the surface water ranged from 16°–18°C, *I. argentinus*' preferred temperature range (Brunetti and Ivanovic 1992). The results showed that higher abundance in the fishery was associated with a lower percent area of confluence front waters in the spawning ground during the spawning season prior to recruitment. This explained about 51% of the variance in abundance. Higher abundance was also associated with a higher percent area occupied by 16°–18°C SST waters on the spawning ground during the spawning season prior to recruitment. This explained about 55% of the variance in abundance. The study suggests that when the confluence front is weak, eggs and paralarvae are retained/transported in the spawning area close to the shelf and that, in common with Sakurai et al.'s (2000) conclusion, recruitment is higher with increased availability of suitable SST habitat.

Dawe et al. (2000), using a seventy-three-year time series of catch and meteorological data illustrated that environmental variability drives *Illex illecebrosus* recruit-

ment. Abundance was positively related to the negative phase of the North Atlantic Oscillation, high water temperature, and southward shifts in the Gulf Stream and the boundary between shelf and offshore slope water. Increased meandering in the Gulf Stream was associated with increased abundance, consistent with observations by Waluda et al. (2001).

Dawe et al.'s (2007) analysis of ocean climate effects on the relative abundance of the squids *I. illecebrosus* and *Loligo pealeii* in the northwest Atlantic Ocean suggests that the efficiency of downstream dispersal of the highly migratory *I. illecebrosus* by the Gulf Stream and the survival of young stages are affected by variation in the latitudinal position of the shelf/slope front. *L. pealeii* population size, however, is favored by higher inshore water temperatures, which explains the range expansion of *L. pealeii* in the year 2000.

Eastern-boundary current systems

The only major fisheries for an ommastrephid squid in an eastern-boundary current system are those for *Dosidicus gigas* in the Eastern Pacific Ocean, and these are pursued off the coast of Peru and in the Gulf of California. Whilst there has been less research effort to understand processes driving variability of squid stocks in the eastern-boundary current systems, this species clearly shows cyclical changes in population size, reflected in fishery catch and catch rates, in relation to the sequence of ENSO events since the early 1990s (Waluda et al. In press; Yamashiro et al. In prep.).

One of the difficulties with understanding *Dosidicus gigas* variability is that its life cycle is less well known than are those of *Illex* spp. and *Todarodes pacificus*. Nevertheless, Waluda and Rodhouse (2006) analyzed interactions between physical conditions on the putative *D. gigas* spawning grounds and abundance in the fishery in the following fishing season. The analysis used Ichii et al.'s (2002) data on the optimum temperature for *D. gigas* hatching (24°–28°C) and assumed that at least one major spawning ground for the species lies in the region of the Costa Rica Dome (Wyrтки 1969), where Vecchione (1999) found large numbers of ommastrephid paralarvae. There was correlation between CPUE in the Peruvian fishery and the proportion of the putative spawning grounds occupied by optimum sea surface temperatures in September, which is when hatching of squid that recruit to the Peru fishery has been shown to occur (Tafur et al. 2001).

ECOLOGICAL CHANGE IN GLOBAL FISHERIES

The effects of ecological change driven by over-exploitation of fishery resources, especially groundfish stocks, on changes in size and geographic range of cephalopod populations have also been considered. Caddy

and Rodhouse (1998) showed that as global groundfish landings decreased over the last three decades of the 20th century, cephalopod landings increased. More specifically, in all but one of fifteen FAO areas, cephalopod landings increased over this time while groundfish landings rose slowly, stabilized, or declined. Cephalopod biomass has not completely replaced fish biomass in the landings, possibly because cephalopod biomass turnover is higher due to a shorter life. The underlying concept is that under intense fishing pressure, groundfish such as hake are likely to be poor competitors with cephalopods which have high growth and reproductive rates, short life cycles, high feeding rates, and voracious predatory habits.

Large-scale range expansion and variability in size of cephalopod populations may have a number of causes, some of which may be natural and/or anthropogenic ocean climate variability and change as well as large-scale ecological change driven by overexploitation of other fish stocks.

DISCUSSION

The recent range expansion of *Dosidicus gigas* in the eastern Pacific Ocean is exceptional and appears to have been triggered by the major ENSO event in 1997–98. Long-lasting physical changes appear to have been triggered by the same event resulting in, among other things, mass shifts of water in the southern Pacific and Indian Oceans at a magnitude sufficient enough for changes in the earth's shape to be detectable by satellite (Dickey et al. 2002). To determine if and how the many oceanic physical, chemical, and biological changes associated with ENSO have influenced the changes in squid stocks will require more sophisticated analyses than have been described in this short review. In most analyses, the physical factors that have been examined explain less than 50% of the variability in squid landings. There is evidence of synchronicity in the abundance of three southern Pacific squid stocks (Waluda et al. 2004). These are all associated with major current systems that are connected to the Antarctic Circumpolar Current. Further, variability in abundance has been found to be correlated with the Southern Oscillation and the Trans Polar Index, so common factors do seem to be involved. Future research will benefit from developing the concept of biological processes, such as range expansion and population explosions, as emergent properties of highly complex systems. The developing field of complexity theory may have much to offer ecologists in this regard. And to understand the processes that drive regime shifts in ocean ecosystems requires at least an understanding of the interactions between change and variability in the ocean climate system and fisheries (Scheffer et al. 2001).

The ENSO system in the Pacific Ocean is one of the better understood variable ocean climate systems in the world. The fisheries along the western seaboard of North and South America are among the best documented. Therefore, the recent *Dosidicus gigas* range expansion and associated changes in the pelagic ecosystem over a very large area provide an opportunity to explore the interacting effects of environmental variability and change as well as ecological change caused by fishing.

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FOOD AND FEEDING OF JUMBO SQUID *DOSIDICUS GIGAS* IN THE CENTRAL GULF OF CALIFORNIA DURING 2005–2007

UNAI MARKAIDA

Línea de Pesquerías Artesanales
El Colegio de la Frontera Sur
Calle 10 # 264, Col. Centro
24000 Campeche, México
umarkaida@ecosur.mx

CÉSAR A. SALINAS-ZAVALA, RIGOBERTO ROSAS-LUIS

Centro de Investigaciones Biológicas del Noroeste (CIBNOR)
Mar Bermejo 195, Colonia Playa Palo de Santa Rita
La Paz, BCS 23090, México

WILLIAM F. GILLY

Hopkins Marine Station of Stanford University
120 Oceanview Blvd.
Pacific Grove, California 93950

J. ASHLEY T. BOOTH

Hopkins Marine Station of Stanford University
120 Oceanview Blvd.
Pacific Grove, California 93950

ABSTRACT

Stomach contents were analyzed for 249 jumbo squid (*Dosidicus gigas*) of 35–80 cm mantle length. All squid were sampled in the central Gulf of California in 2005–07, primarily on the commercial fishing grounds of Santa Rosalia during different times of the year. Diet off Santa Rosalia was mainly composed of mesopelagic micronektonic organisms, mostly the myctophids *Benthoosema panamense*, *Triphoturus mexicanus*, and the squid *Pterygioteuthis giardi*. Pteropods and crustaceans made up a smaller portion of the diet. Squid sampled elsewhere revealed that the pelagic red crab, *Pleuroncodes planipes*, and northern anchovy, *Engraulis mordax*, could also be major dietary items. Cannibalism incidence increased with squid mantle length. We propose that the main prey of jumbo squid in the central Gulf of California derives from the mesopelagic community associated with the upper boundary of the oxygen minimum layer, a well-developed midwater feature in this region. In addition, opportunistic foraging on a variety of organisms supplements their dietary intake. These data are discussed in conjunction with recent electronic tagging data that revealed vertical and horizontal movements of jumbo squid. This work demonstrates a need to study the dynamics of the oxygen minimum layer and the composition of the deep-scattering layer over the upper slope of Guaymas basin.

INTRODUCTION

The first phase of commercial fishing for jumbo squid, *Dosidicus gigas*, in the Gulf of California began in 1974 and ended in 1981 (Ehrhardt et al. 1983). The fishery collapsed during and after the strong 1982–83 El Niño. Up to that time, stomach content analysis showed that jumbo squid from the Gulf fed mainly on neritic and small pelagic fishes (sardines, mackerels), pelagic red crab, and myctophids, with cannibalism also occurring (García-Domínguez and González-Ramírez 1988, Ehrhardt 1991). Ehrhardt (1991) therefore suggested that jumbo squid may have effects on the important commercial sar-

dine resource. This paper is arguably the most historically influential study of *Dosidicus* diet, and the conclusion of sardine predation has been widely cited in reviews on cephalopod feeding (see Boyle and Rodhouse, 2005).

A largely artisanal fishery resumed in 1994 for a form of *D. gigas* that matures at a large size (40–85 cm mantle length, ML), operating close to shore in the Guaymas Basin, both in the States of Sonora and Baja California Sur. Annual landings were over 100,000 tonnes in 1995–97. During this period most squid were taken off Santa Rosalia, Baja California, between May and November, and the remaining off Guaymas, Sonora, between December and April (Markaida and Sosa-Nishizaki 2001). In contrast to results of earlier studies, Markaida and Sosa-Nishizaki (2003) found that these large squid fed mostly on mesopelagic micronekton, mainly myctophids.

The squid fishery in the central Gulf collapsed again in 1998 following the 1997–98 El Niño. Smaller squid that matured at <45 cm ML re-established the fishery in the following year after a transition to La Niña conditions. These smaller squid again fed mostly on myctophids (Markaida 2006). Since 2000, large squid have again dominated the fishery in the central Gulf (Nevárez-Martínez et al. 2006; Bazzino et al. 2007), but dietary studies have not been reported during this period.

This paper presents an analysis of jumbo squid feeding in the central Gulf of California during the period of 2005–07 based on samples made on the commercial fishing grounds off Santa Rosalia during different times of the year and on samples opportunistically collected from elsewhere in the Gulf. Diet was mainly composed of mesopelagic micronekton, primarily myctophid fishes. Although opportunistic foraging on anchovies and other small fishes does occur, no evidence of sardine predation was found.

Recently (since 2002), *Dosidicus gigas* has undergone a major northern range expansion to as far north as southeast Alaska (Wing 2006). Because *Dosidicus gigas* is an abundant and highly migratory predator, shifts in diet