Tagging studies on the jumbo squid (*Dosidicus gigas*) in the Gulf of California, Mexico

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Dosidicus gigas, the only species in the genus *Dosidicus*, is commonly known as the jumbo squid, jumbo flying squid (FAO, see Roper et al., 1984), or Humboldt squid. It is the largest ommastrephid squid and is endemic to the Eastern Pacific, ranging from northern California to southern Chile and to 140°W at the equator (Nesis, 1983; Nigmatullin, et al., 2001). During the last two decades it has become an extremely important fisheries resource in the Gulf of California (Ehrhardt et al., 1983; Morales-Bojórquez et al., 2001), around the Costa Rica Dome (Ichii et al., 2002) and off Peru (Taipe et al., 2001). It is also an active predator that undoubtedly has an important impact on local ecology in areas where it is abundant (Ehrhardt et al., 1983; Nesis, 1983; Nigmatullin et al., 2001; Markaida and Sosa-Nishizaki, 2003).

Ommastrephid squid, including the jumbo squid, are largely pelagic and may migrate long distances as part of their life cycle (Mangold, 1976). A general pattern of long-distance migration for the jumbo squid over its entire range was proposed by Nesis (1983) and smaller-scale migrations within the Gulf of California have also been proposed according to the distribution of the fishery during 1979–80 (Klett, 1982; Ehrhardt et al., 1983). During this period squid were reported to enter the Gulf from the Pacific in January, to reach their northernmost limit (29°N) by April, and to remain in the central Gulf from May through August; the highest concentrations were found along the western (Baja California) coast. From September onward these squid appear to migrate eastward to the Mexican mainland coast and then southwards, to the mouth of the Gulf and back into the Pacific (Klett, 1982; Ehrhardt et al., 1983).

Since 1994 a seasonal pattern in the jumbo squid fishery has emerged in which large squid are abundant in the central Gulf essentially all year. During November to May, the fishery is centered in the area of Guaymas. In Sta. Rosalia the fishery operates from May to November, which is also the period of peak landings (see Fig. 1; SEMARNAP, 1996, 1997, 1998, 1999, 2000; SAGARPA, 2001; SAGARPA[1]) (see also Markaida and Sosa-Nishizaki, 2001). These generally reciprocal landing patterns are consistent with the abundance patterns described by Klett (1982), although the exact migrations proposed by Ehrhardt et al. (1983) have never been directly observed (Morales-Bojórquez et al., 2001).

All these studies concerning jumbo squid migrations have relied on analyses of landing statistics and catch data acquired by fishing stations on commercial squid-jigging vessels. Although migratory patterns of several other ommastrephid species of commercial importance have been directly demonstrated with conventional tag-and-recapture methods (Nagasawa et al., 1993), to our knowledge jumbo squid has not been studied in this manner. Given the commercial and ecological importance of this species, such studies would be valuable.

This paper describes conventional tag-and-recapture experiments on jumbo squid in the central Gulf of California. Tag-return rates were higher than in most previous studies of other ommastrephid species, and seasonal migrations between the Sta. Rosalia and Guaymas areas were directly demonstrated. Growth rates were also directly determined for the first time.

[1] SAGARPA (Secretaría de agricultura, ganadería, desarrollo rural, pesca y alimentación). Anuario Estadístico de Pesca, http://www.sagarpa.gob.mx/conapesca/planeacion/anuario/anuario2001.zip and http://www.sagarpa.gob.mx/conapesca/planeacion/anuario2002. [Accessed 26 July 2004.]

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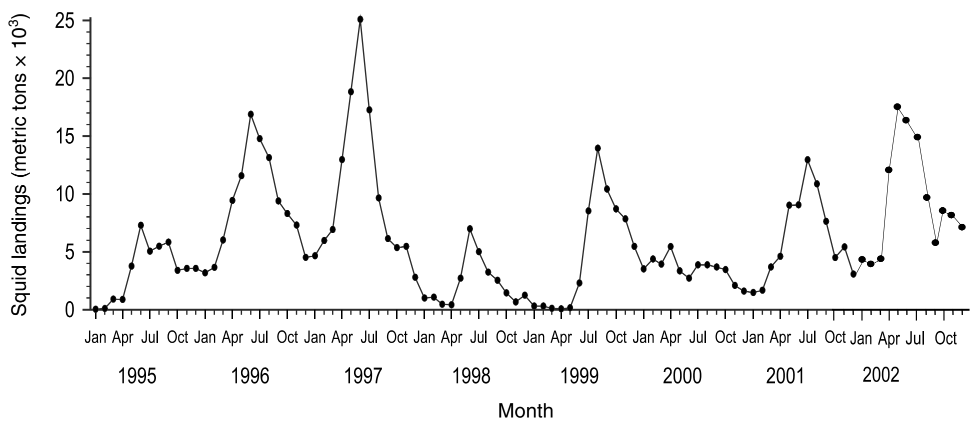

Figure 1

Monthly landings (in metric tons) of *Dosidicus gigas* in Mexico from 1995 through 2002.

Materials and methods

Fieldwork was carried out in two separate experiments along both coasts of the Guaymas basin (see Fig. 2). This area of the central part of the Gulf of California accounts for more than 95% of Mexican jumbo squid landings. A total of 996 squid were tagged between 9 and 16 October 2001, in the general vicinity of Sta. Rosalia, Baja California Sur (B.C.S.), as indicated in Figure 2. Another 997 squid were tagged off Guaymas, Sonora, between 3 and 7 April 2002. Both experiments were conducted close to the anticipated end of the respective fishing seasons for each zone, because we hoped to obtain recaptures both locally and from more distant sites after the squid had migrated away from the fishing areas.

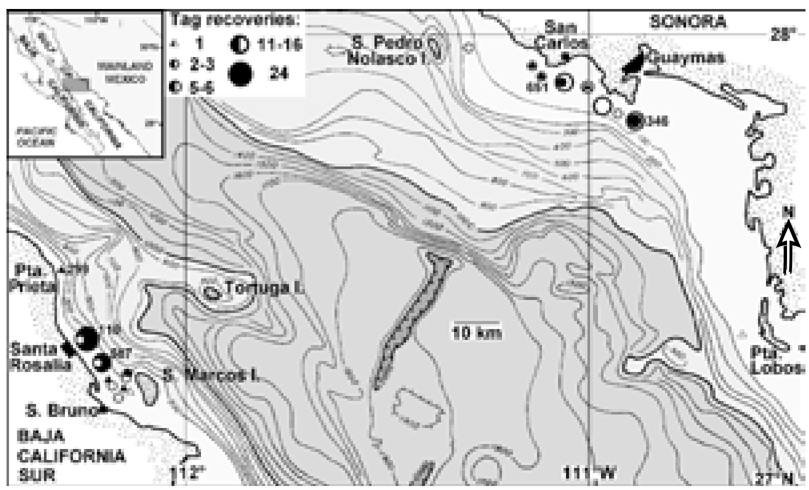

Figure 2

Map of the Guaymas basin in the central Gulf of California showing both coasts where the tagging experiments were performed**.** Area of detailed main map is indicated by a gray rectangle in upper leftmost inset. Numbers of tags deployed are in bold type in main map. Symbols for the numbers of tags recovered are indicated in the inset "Tag recoveries." Black symbols represent squid tagged off Sta. Rosalia; white symbols represent squid tagged off Guaymas. Depth contours are in meters. Adapted from Bischoff and Niemitz (1980).

Squid were caught by commercial fishermen using hand-lines with 30-cm jigs and were tagged on deck with spaghetti-type, plastic cinch-up tags (Floy Tag Co., Seattle, WA) through the anterior edge of the dorsal mantle. This process took about 30 seconds, and the squid was then immediately released. All squid quickly jetted away with no obvious sign of trauma or physical impairment. Animals with any visible damage, primarily form cannibalistic attacks by other squid, were not tagged. In addition, dorsal mantle length (ML) was measured to the nearest mm for all squid in the Guaymas experiment.

Tag-return information was imprinted on the tag, and posters announcing the experiment were distributed at squid-landing ports and at local processing facilities in Sta. Rosalia, San Lucas, San Bruno, Mulege, Loreto and La Paz (B.C.S.), as well as in San Carlos, Guaymas, Yavaros (Sonora) and Mazatlan (Sinaloa) (Fig. 2). A monetary reward ($50 US) was offered for each tag returned with information on recapture date and location. During the second experiment an additional reward was offered for information on squid ML and stage of sexual maturity as defined by Lipinski and Underhill (1995): immature (stages I–II), maturing (III) and mature (IV–V). Average daily growth rate (DGR) was calculated from the increase in ML between tagging and recapture divided by the number of days elapsed during this period.

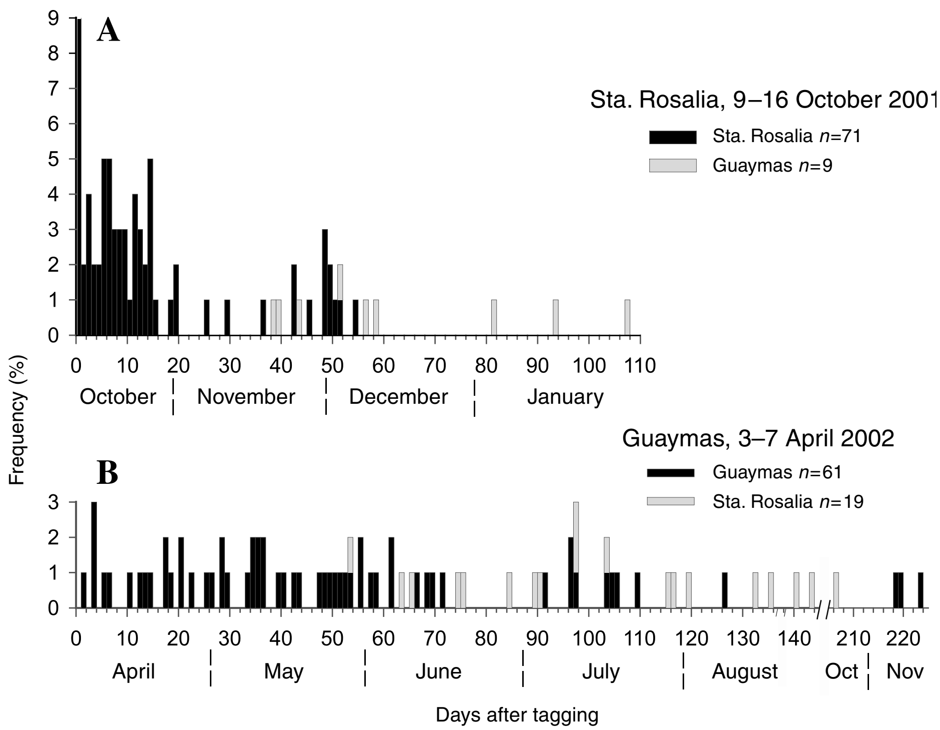

Figure 3

Time course for recapture data for squid tagged off Santa Rosalia (**A**) and off Guaymas (**B**). In both sections, black bars represent squid recaptured from the same coast where tagging was done, and gray bars represent squid recaptured from the opposite coast. Note that a gap exists between August and October in panel B.

Results

Timing of tag returns

A total of 80 tags (8.03%) were recovered for the squid tagged off Sta. Rosalia. Of these, 71 were recovered in the general vicinity of this port. More than a third of these tags (25) were discovered at commercial squid processing plants, where the mantles are manually cleaned before final processing. Squid were captured generally shortly after tagging; most of the tags (52) were recovered during the first 15 days (Fig. 3A). The shortest recapture period was only several hours. In this case, a squid tagged by the crew of one of our boats was caught about one km away by our second boat.

In addition to the Sta. Rosalia returns, another nine squid (0.9%) were recaptured off Guaymas, from 39 to 108 days after tagging (Fig. 3A). The temporal overlap in returns from the two localities (days 39–55) and the total lack of any subsequent Sta. Rosalia returns would indicate that a significant number, if not most, of the squid migrated from Sta. Rosalia to Guaymas and potentially elsewhere during this period (17 Nov–4 Dec).

In the second experiment, conducted off Guaymas, 80 tags (8%) were also recovered. Sixty-one were recovered in the Guaymas area over an extended period from 2 to 224 days after tagging (Fig. 3B). In this case, the squid were recaptured more or less constantly at a low rate over the first 60 days. Surprisingly, only one tag was recovered at a processing plant during this period. Sporadic returns then continued in Guaymas over the next three months. It should be noted that there was little squid fishing activity in the area during September because of the beginning of the commercial shrimp season. The final three tags were recovered after 219–224 days (8–13 Nov). These squid were tagged on the same night and location seven months earlier.

Of the tags deployed in Guaymas, 19 (1.9%) were recovered in the Sta. Rosalia area in summer 2002 (28 May–29 August) from 54 to 207 days after tagging (Fig. 3B). Seven of these tags were recovered at squid factories. A period of overlapping returns occurred over days 54–72, and we interpreted this overlap in returns as being consistent with a seasonal mass migration form Guaymas to Sta. Rosalia. A second period of overlapping returns of similar duration occurred in July. However, in this case, returns from Guaymas continued throughout the entire summer and into the fall. It thus appears that some squid remained in the Guaymas area during this period.

Dependence of recapture rate on squid size

Squid tagged off Guaymas ranged from 32.7 to 83 cm ML (mean [±SD] of 56.6 [±7.5] cm ML [Fig. 4]). Recapture rate is clearly size dependent. No squid smaller than 46 cm ML were recaptured, and recapture rates were low (1.3–3.4%) for squid of 46–50 cm ML. However, recapture increased in roughly direct proportion to ML, reaching 15–20% for squid >70 cm ML.

Determination of daily growth rate (DGR)

Dorsal ML was measured from forty-four squid tagged off Guaymas after recapture at 4 to 224 days. ML values ranged between 46 and 80.7 cm. Variability in DGR determination, as indicated by the standard deviation (SD) of binned data from 20-day intervals, clearly decreased as the time to recapture increased. Thus, a significant negative correlation exists between the SD of DGR and recovery time (r^2=0.88, P<0.01, n=6) (Fig. 5). Six measurements of squid caught before 40 days yielded negative growth rates. This finding indicates that large discrepancies in DGR calculations exist in measurements on squid with short recapture times, because any errors in ML measurement are generally much larger. Growth rate estimates from squid captured after 40 days yielded values of 1.0–1.5 mm/day (SD of 0.05–0.6). We regard these as the only reliable data.

Further analysis of DGR was limited to squid captured after 40 days. Figure 6 illustrates DGR versus "mean" ML (average of ML at times of tagging and recapture) for selected squid of different sexes and stages of maturity. Probably the most reliable DGR estimates come from the four squid that grew from 47–53 to 71–74 cm ML in 207–224 days, and these measurements yield a mean DGR of 1.05 [±0.05] mm/day (Fig. 5 and ▽ in Fig. 6). Solid and dashed curves in Figure 6 represent DGR independently determined for both sexes through analysis of statolith increments (Markaida et al., 2004) for squid of a comparable size range. These growth rates are about twice those determined in the present study by direct ML measurements.

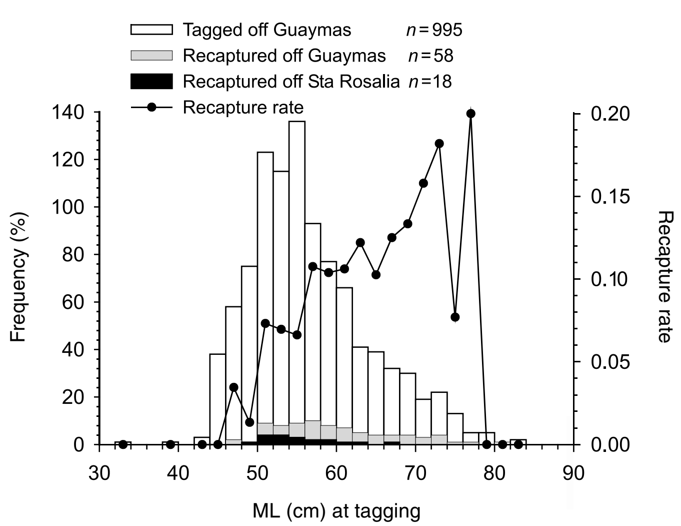

Figure 4

Mantle length (ML) distribution for all squid tagged off Guaymas (white bars) and for those recaptured off Guaymas (gray bars) and Santa Rosalia (black bars). Black circles represent recapture rate.

Discussion

Tag return rates

High recovery rates obtained in our study clearly demonstrate that *D. gigas* in the Gulf of California is suitable for tagging studies. This large species is relatively easily tagged with conventional plastic tags, and the tagging operation produced no obviously deleterious effects on the squid. These features make jumbo squid an attractive species for application of archival electronic tags or telemetry devices.

Despite extensive tagging efforts and intense commercial fisheries, recapture rates for other species of ommastrephid squid have generally been much lower. In the extreme case, no recaptures whatsoever were obtained for the northern shortfin squid (*Illex illecebrosus*) tagged in offshore waters of Newfoundland (Hurley and Dawe, 1981). In other studies recaptures ranged from 0.03–0.1% for the Argentine shortfin squid (*I. argentinus*) in the Southwest Atlantic (Brunetti et al., 2000), to 1.0–6.2% for the European flying squid (*Todarodes sagittatus*) off Norway (Wiborg et al.[2]). The neon flying squid (*Ommastrephes bartramii*) from the North Pacific also yielded low rates (0.1–0.5%; Murata and Nakamura, 1998; see also Nagasawa et al., 1993). In 62 years of tagging studies of Japanese flying squid (*Todarodes pacificus*), only a few experiments carried out in the Sea of Japan and Tsugaru Strait yielded return rates that match those of the present study (up to 16.4%; see Nagasawa et al., 1993). The highest tag recovery rate (19–32%) was found for the northern shortfin squid in Newfoundland inshore areas (Hurley and Dawe, 1981). Recapture rates of up to 12.7% have also been reported for large, neritic loliginid squid (Nagasawa et al., 1993; Sauer et al., 2000).

In the present study, recapture rate was found to be directly proportional to mantle length, ranging from <3.5% for squid <50 cm

[2] Wiborg, K. F., J. Gjøsaeter, I. M. Beck, and P. Fossum. 1982. The squid *Todarodes sagittatus* (Lamarck). Distribution and biology in Northern waters, August 1981–April 1982. Council Meet. Int. Coun. Explor. Sea (K:30):1–17. ICES, Palægade 2-4, DK-1261, Copenhagen K, Denmark. info@ices.dk.

ML to 20% for squid close to 80 cm ML (Fig. 4). Reasons for this strong size-dependence are not clear. Smaller squid may either suffer a higher natural mortality rate or migrate southward out of the Guaymas basin more readily than the larger squid. We do not believe that the tagging process itself leads to such a difference in mortality rate, but this possibility cannot be ruled out.

Several factors are relevant to evaluating differences in recapture rates for jumbo squid and other ommastrephids. First, squid of the other species are not as large as jumbo squid. We are not aware of any other published data on size-dependence of recapture rates, but this phenomenon may be relevant. Second, the localized nature of the fisheries surrounding the Guaymas basin equates with high concentrations of squid in relatively small areas that are intensively fished. Most recent tagging studies of other ommastrephids have taken place in oceanic waters in the Sea of Japan and North Pacific, where the fishing zone is extremely large and far from any localized coastal fishing areas (Nagasawa et al, 1993). The extreme disparity in return rates for nearshore versus offshore studies in Newfoundland supports this idea. Third, an ambitious advertising campaign (posters) and the substantial reward offered for tag returns undoubtedly stimulated a high degree of cooperation in the largely artisanal Mexican fishery that is highly concentrated in Sta. Rosalia and Guaymas. A strong dependence of tag-return rate on rewards and advertising has been previously noted (see Nagasawa et al., 1993).

Seasonal migration

Results from this study directly demonstrate that jumbo squid in the Guaymas basin migrate across the Gulf on a seasonal basis. Squid appear to migrate from Sta. Rosalia to Guaymas during the second half of November and early December and to make the reverse trip in late May and early June. Thus, large squid (40–80 cm ML) remain available to fisheries surrounding the Guaymas basin throughout the year. These data support the idea that these fishing areas are feeding grounds (Markaida and Sosa-Nishizaki, 2001). What fraction of squid, if any, migrate southward out of the Guaymas basin and potentially into the Pacific cannot be ascertained from our data.

Transit time across the Gulf for the migrating squid appears to be fairly brief—probably less than 16 days based on the overlap of recaptures in both fishing areas. Assuming a straight-line distance of 130 km between

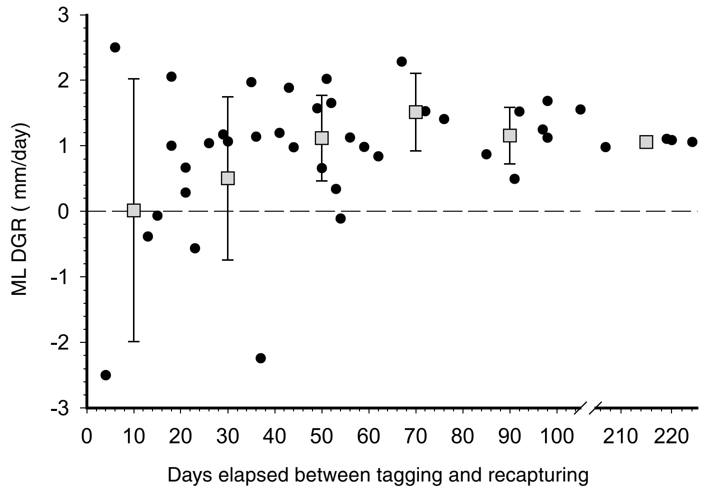

Figure 5

Daily growth rate (DGR) in mantle length (ML) determined for squid recaptured at different times after tagging. Black circles represent measurements from individual animals. Gray squares represent means ±1 SD for squid grouped in 20-day bins. Note that a gap exists between 100 and 200 days.

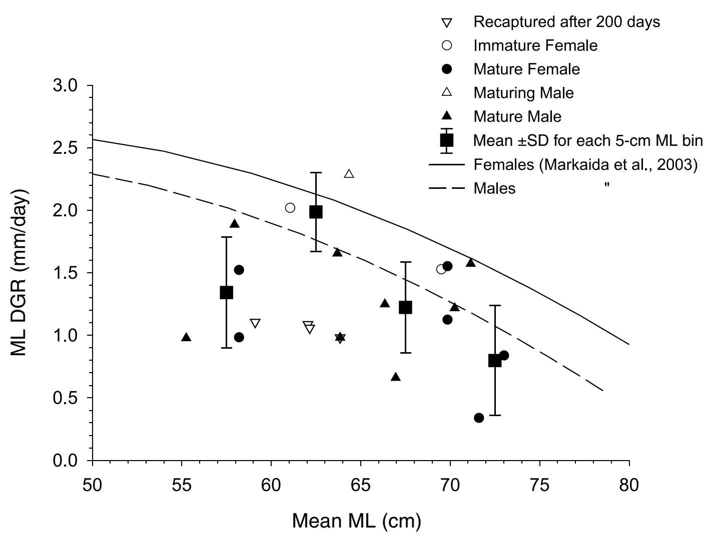

Figure 6

Relationship of daily growth rate (DGR) and mean mantle length (ML) (average of measured ML at time of tagging and time of recapture). Small symbols represent measurements from selected individual animals as follows: squid recaptured after >200 days (▽), immature female (○), mature female (●), maturing male (△), mature male (▲). Larger squares (■) indicate means ±1 SD for all data pooled into 5-cm bins. Analysis was limited to squid recaptured after 40 days and of identified sex. Curves represent DGR vs. ML relationship as determined by counting statolith increments for females (solid) and males (dashed) and are adapted from Markaida et al. (2004).

these areas, the average maintained speed during the migration would be about 8 km/day. A comparable figure can be derived from one of our first squid to be recaptured. This animal was tagged at Pt. Prieta (see Fig. 2) and recaptured 20 km away off Sta. Rosalia (Fig. 2) after three days.

This estimated velocity for a trans-Gulf migration is well within the range of rates observed in other studies of ommastrephids (O'Dor, 1988). Jumbo squid tracked with acoustic telemetry off Peru covered 3–5 miles in 8–14 hours, or about 14 km/day (Yatsu et al., 1999). Neon flying squid tracked in the same way covered up to 22 km per day (Nakamura, 1993). Migration rates obtained from tagging studies yielded even higher estimates. Maximum speed for migrating short-finned squid has been estimated at 20–30 km/day (Dawe et al., 1981; Hurley and Dawe, 1981), and high rates have also been reported for the Japanese squid (see Nagasawa et al., 1993). Large loliginid squid have been reported to migrate at rates of 3 to 17 km/day (see Sauer et al., 2000).

Daily growth rates

Variance in DGR estimates from ML measurements decreased dramatically after 30 days after tagging, and became fairly consistent by 50 days. Clearly, estimates of DGR in our study are only reliable for these later times, and a DGR of 1–1.5 mm/day in ML is evident for squid in the 50–70 cm range of ML (Fig. 6). These absolute rates would correspond to relative rates of 0.15–0.22% increase in ML per day.

There are few comparable estimates of growth rates for other ommastrephid squids based on tag-recapture studies. However, the neon flying squid grows 0.5–2.7 mm/day in the 18–48 cm ML range (Araya, 1983), and good agreement exists between growth rates obtained from tag-recapture studies and those from statolith aging studies (Yatsu et al., 1997). When converted to relative growth rate, this species would thus appear to grow substantially faster than the jumbo squid. The common Japanese squid grows 0.45 mm/day (Nagasawa et al., 1993), but for this species, mantle lengths were not given; therefore relative rates cannot be estimated.

More importantly, absolute growth rates determined by direct ML measurements in the present study disagreed with those derived from statolith aging methods (Markaida et al., 2004), and this discrepancy merits re-evaluation of previous longevity estimates. Squid of 50 cm ML are thought to be about 260 days old based on statolith ring counts, and our tag-recapture study revealed that it can take another 200 days to grow to 70 cm ML. The estimated age at this size would therefore be 460 days, about 100 days more than that estimated by statolith aging for squid of 70 cm ML (Markaida et al., 2004). Thus, the largest squid found in the Gulf of California (about 90 cm ML) might be up to 2 years old.

Reasons for the apparent underestimates in longevity with statolith aging are unclear. Difficulty in resolving discrete rings late in life of a specimen is one possibility. Another is that the assumed daily ring deposition may not occur throughout the lifetime of a jumbo squid. No successful validation studies have been reported for this species, either in the laboratory or in the wild.

Squid distributions in the Gulf in relation to commercial landings

Although large-scale migrations of jumbo squid within the Guaymas basin are apparently responsible for the seasonal pattern in the commercial landings (Fig. 1; see also Markaida and Sosa-Nishizaki, 2001), the biological and oceanographic reasons for these migrations are not well established. The reciprocal pattern in squid distribution between the eastern and western central Gulf is correlated with the wind-driven upwelling seasonality in this area (Roden and Groves, 1959) and is probably highly influenced by this oceanographic feature. A similar situation exists in the life cycle of another important pelagic resource, the Pacific sardine (*Sardinops caeruleus*) (Hammann et al., 1988).

However, other biological factors are also probably important. Summer upwelling in the western Gulf is actually less intense than off the eastern coast in winter (Hammann et al., 1988; Santamaría-del-Angel et al., 1999), yet 80% of squid landings were made at Sta. Rosalia between 1995 and 1997 (Markaida and Sosa-Nishizaki, 2001). We propose that concentrations of spawning myctophids (lanternfishes) off Baja California in the summer (Moser et al., 1974) may be largely responsible for this disparity because these fish are a major prey item for squid in the Guaymas basin (Markaida and Sosa-Nishizaki, 2003).

Data in the present study also indicate that jumbo squid may be available to commercial fishing efforts off each coast for a longer period than previously thought. Our data indicate that squid were recovered in the waters off Guaymas throughout the year; therefore it is likely that some squid do not undergo the westward spring migration (Fig. 3B). However, it is not certain that the final returns from Guaymas after 7 months were of this resident stock, because they would have had time to migrate to Sta. Rosalia and back again. It is also unclear whether a resident stock of squid exists in the Sta. Rosalia area year-round. Strong northern winds in this area lead to a cessation of commercial fishing efforts during the winter months, and the lack of tag returns during winter may simply reflect this fact.

Long-distance migrations into and out of the Gulf of California

Although data in this paper have demonstrated seasonal migrations of jumbo squid within the Guaymas basin, migration patterns into this region from the southern Gulf and open Pacific (and back out) remain unknown. The much lower level of commercial fishing effort in these latter areas will greatly constrain efforts to elucidate migrations over these longer distances using conventional tag-and-recapture approaches.

Presumably, as the largest eunektonic squid, jumbo squid should be able to perform large-scale migrations covering its whole geographic range as do other ommastrephids (O'Dor, 1988). The high tag return rates achieved in the present study, in conjunction with the large size of the squid, make application of a variety of archival electronic tagging devices an attractive possibility. Such devices could reveal long-distance migrations across the large range of jumbo squid in a fishery-independent manner.

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Literature cited

Araya, H.
1983. Fishery, biology and stock assessment of *Ommastrephes bartrami* in the North Pacific Ocean. Mem. Nat. Mus. Victoria 44:269–283.

Bischoff, J. L., and J. W. Niemitz.
1980. Bathymetric maps of the Gulf of California: bathymetry of the Central Gulf Province, Map I-244. Miscellaneous Investigation Series, U. S. Geological Survey, Denver, CO. Sheet 3 of 4 sheets.

Brunetti, N. E., M. L. Ivanovic, G. R. Rossi, B. Elena, H. Benavides, R. Guerrero, G. Blanco, C. Marchetti, and R. Piñero.
2000. JAMARC-INIDEP joint research cruise on Argentine short-finned squid (*Illex argentinus*). January-March 1997. Argentine Final Report. INIDEP Inf. Tec. 34:1–36.

Dawe, E. G., P. C. Beck, H. S. Drew, and G. H. Winter.
1981. Long distance migration of a short-finned squid *Illex illecebrosus*. J. Northwest Atlantic Fish. Sci. 2:75-76.

Ehrhardt, N. M., P. S. Jacquemin, F. García B., G. González D., J. M. López B., J. Ortiz C. and A. Solís N.
1983. On the fishery and biology of the giant squid *Dosidicus gigas* in the Gulf of California, Mexico. *In* Advances in assessment of world cephalopod resources (J. F. Caddy, ed.), p. 306–339. FAO Fish. Tech. Pap. 231.

Hammann, M.G., T. R. Baumgartner, and A. Badan-Dangon.
1988. Coupling of the Pacific sardine (*Sardinops sagax caeruleus*) life cycle with the Gulf of California pelagic environment. CalCOFI Rep. 29:102–109.

Hurley, G. V., and E. G. Dawe.
1981. Tagging studies on squid (*Illex illecebrosus*) in the Newfoundland area. North Atlantic Fisheries Organization (NAFO) SCR Doc., No. 80/II/33, serial no. 072, 11 p. NAFO, Dartmouth, Nova Scotia, Canada.

Ichii, T., K. Mahapatra, T. Watanabe, A. Yatsu, D. Inagake, and Y. Okada.
2002. Occurrence of jumbo flying squid *Dosidicus gigas* aggregations associated with the countercurrent ridge off the Costa Rica Dome during 1997 El Niño and 1999 La Niña. Mar. Ecol. Prog. Ser. 231:151–166.

Klett, A.
1982. Jumbo squid fishery in the Gulf of California, Mexico. *In* Proceedings of the International Squid Symposium, August 9–12, 1981, Boston, Massachusetts (prepared by the New-England Fisheries Development Found., Inc.), p. 81–100. UNIPUB, New York, NY.

Lipinski, M. R., and L. G. Underhill.
1995. Sexual maturation in squid: Quantum or continuum? S. Afr. J. Mar. Sci. 15:207–223.

Mangold, K.
1976. La migration chez les Céphalopodes. Oceanis 2(8):381–389. [In French.]

Markaida, U., and O. Sosa-Nishizaki.
2001. Reproductive biology of jumbo squid *Dosidicus gigas* in the Gulf of California, 1995–1997. Fish. Res. 54(1):63–82.
2003. Food and feeding habits of jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae) from the Gulf of California, Mexico. J. Mar. Biol. Assoc. U.K. 83:507–522.

Markaida, U., C. Quiñónez-Velázquez, and O. Sosa-Nishizaki.
2004. Age, growth and maturation of jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae) from the Gulf of California, Mexico. Fish. Res. 66(1):31–47

Morales-Bojórquez, E., M. A. Cisneros-Mata, M. O. Nevárez-Martínez and A. Hernández-Herrera.
2001. Review of the stock assessment and fishery biology of *Dosidicus gigas* in the Gulf of California, México. Fish. Res. 54:83–94.

Moser, H. G., E. H. Ahlstrom, D. Kramer, and E. G. Stevens.
1974. Distribution and abundance of fish eggs and larvae in the Gulf of California. CalCOFI Rep. 17:112–128.

Murata, M., and Y. Nakamura.
1998. Seasonal migration and diel vertical migration of the neon flying squid, *Ommastrephes bartramii*, in the North Pacific. *In* Contributed papers to the international symposium on large pelagic squids, Tokyo, July 18–19, 1996 (T. Okutani, ed.), p. 13–30. Japan Marine Fishery Resources Research Center (JAMARC).

Nakamura, Y.
1993. Vertical and horizontal movements of mature females of *Ommastrephes bartramii* observed by ultrasonic telemetry. *In* Recent advances in cephalopod fisheries biology: contributed papers to 1991 CIAC international symposium and proceedings of the workshop on age, growth and population structure (T. Okutani, R. K. O'Dor, and T. Kubodera, eds.), p. 331–336. Tokay Univ. Press, Tokyo, Japan.

Nagasawa, K., S. Takayanagi, and T. Takami.
1993. Cephalopod tagging and marking in Japan: a review. *In* Recent advances in cephalopod fisheries

biology: contributed papers to the 1991 Cephalopod International Advisory Council (CIAC) international symposium and proceedings of the workshop on age, growth, and population structure (T. Okutani, R. K. O'Dor, and T. Kubodera, eds.), p. 313–329. Tokay Univ. Press, Tokyo, Japan.

Nesis, K. N.
1983. *Dosidicus gigas*. *In* Cephalopod life cycles, vol. I, species accounts (P. R. Boyle, ed), p. 215–231. Academic Press, London, UK.

Nigmatullin, Ch. M., K. N. Nesis, and A. I. Arkhipkin.
2001. A review of the biology of the jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae). Fish. Res. 54:9–19.

O'Dor, R. K.
1988. The energetic limits on squid distributions. Malacologia 29(1):113-119.

Roden, G. I., and G. W. Groves.
1959. Recent oceanographic investigations in the Gulf of California. J. Mar. Res. 18:10–35.

Roper, F. E., M. J. Sweeney, and C. E. Nauen.
1984. FAO species catalogue: vol. 3, Cephalopods of the world, 272 p. FAO, Rome.

SAGARPA (Secretaría de agricultura, ganadería, desarrollo rural, pesca y alimentación).
2001. Anuario estadístico de pesca 2000. SAGARPA-CONAPESCA (Comisión Nacional de Acuacultura y Pesca), Mexico, 268 p. [In Spanish.]

Santamaría-del-Angel, E., S. Álvarez-Borrego, R. Millán-Núñez, and F. E. Müller-Karger.
1999. On the weak effect of summer upwelling on the phytoplankton biomass of the Gulf of California. Rev. Soc. Mex. Hist. Nat. 49:207–212. [In Spanish, English abstract.]

Sauer, W. H. H., M. R. Lipinski, and C. J. Augustyn.
2000. Tag recapture studies of the chokka squid *Loligo vulgaris reynaudii* d'Orbigny, 1845 on inshore spawning grounds on the south-east coast of South Africa. Fish. Res. 45:283–289.

SEMARNAP (Secretaria del medio ambiente, recursos naturales y pesca). Distributed by the Mexican Secretary on Natural Resources.
1996. Anuario estadístico de pesca 1995, 235 p. SEMARNAP, Mexico. [In Spanish.]
1997. Anuario estadístico de pesca 1996, 232 p. SEMARNAP, Mexico. [In Spanish.]
1998. Anuario estadístico de pesca 1997, 241 p. SEMARNAP, Mexico. [In Spanish.]
1999. Anuario estadístico de pesca 1998, 244 p. SEMARNAP, Mexico. [In Spanish.]
2000. Anuario estadístico de pesca 1999, 271 p. SEMARNAP, Mexico. [In Spanish.]

Taipe, A., C. Yamashiro, L. Mariategui, P. Rojas, and C. Roque.
2001. Distribution and concentrations of jumbo flying squid (*Dosidicus gigas*) off the Peruvian coast between 1991 and 1999. Fish. Res. 54:21–32.

Yatsu, A., S. Midorikawa, T. Shimada, and Y. Uozumi.
1997. Age and growth of the neon flying squid, *Ommastrephes bartrami*, in the North Pacific Ocean. Fish. Res. 29:257–270.

Yatsu, A., K. Yamanaka, and C. Yamashiro.
1999. Tracking experiments of the jumbo squid, *Dosidicus gigas*, with an ultrasonic telemetry system in the Eastern Pacific Ocean. Bull. Nat. Res. Inst. Far Seas Fish. 36:55–60.