

RESEARCH INTO THE LIFE HISTORY OF *LOLIGO OPALESCENS*: WHERE TO FROM HERE?

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ABSTRACT

Statolith ageing techniques have greatly aided our understanding of loliginid squid biology. We now know that life spans of loliginid squids are relatively short: most temperate species live for about a year or slightly more. Many tropical species appear to complete their life spans in fewer than 200 days. Early growth estimates for *Loligo opalescens* based on length-frequency analysis have suggested a life span of around two years. However, preliminary data from statolith ageing and culture of *L. opalescens* have shown that reproductive maturity can be reached in less than a year. Further research is needed to determine the life span of this species, but it is possible that it may not exceed one year. Research is especially needed to validate periodicity in statolith increments and to study latitudinal and seasonal variation in growth and maturity rates. This will provide the necessary data for future management and policy decisions. Other areas of research—the use of predators as sampling tools; investigation of the condition of and degradation of tissue in association with maturity; tracking studies using transmitters, radio acoustic positioning, and telemetry (RAPT) as well as traditional tagging; and light trapping—may yield important biological data about *L. opalescens*.

INTRODUCTION

Loliginid squid stocks occur in most continental shelf areas of the world's oceans except for the extreme polar regions. Some species have a wide latitudinal distribution, such as *Loligo opalescens* off the west coast of North America or *Loligo forbesi* in European/African waters. In contrast, *Sepioteuthis australis*, which is restricted to southern Australia and northern New Zealand waters, is an example of a loliginid with a much narrower distribution. In some continental shelf regions (e.g., northern Australia; Yeatman and Benzie 1993, 1994, or the Gulf of Thailand; Chotiyaputta 1993) there is a diversity of loliginid species, whereas in other regions there is only one loliginid species, such as *L. gahi* on the Patagonian Shelf and *L. opalescens* off California.

Many of these populations are coming under increasing pressure from national and international fisheries. There is a need to obtain information on the biology and life

history of these loliginid populations worldwide to provide the necessary building blocks for management and policy decisions. Without such data, management is based only on guesses and approximations. Current knowledge about the age and growth of loliginid squids has revealed that previous life span estimates have led to an inaccurate understanding of the biology of these organisms. One example of this has been the application of length-frequency analysis in an attempt to determine squid growth (see Jackson and Choat 1992; Jackson et al. 1997). The results of such analysis have led to the measurement of life spans in years instead of days. Such errors can have profound implications for interpreting population dynamics and for management decisions.

The collection of accurate data on age, growth, and life history is fundamental for implementing long-term management strategies. This paper reports on past research into the age, growth, and life history of *L. opalescens*; identifies where we are now; and suggests areas where research should be focused. The significance of applying ageing techniques to *L. opalescens* can be appreciated by drawing on the results of studies from other loliginid populations (summarized in table 1) that have used similar ageing techniques to determine important biological features.

Loligo opalescens is not only a valuable fishery resource but also an important ecological species in the California Current. Its predators include at least 19 species of fish, 13 species of birds, and 8 species of marine mammals (Morejohn et al. 1978). Some vertebrates reviewed in Morejohn et al. (1978) that appear to be major predators of *L. opalescens* include the fish curlfin turbot (*Pleuronichthys decurrens*), several specimens of which have been shown to consume more than 600 individual squid; the seabirds rhinoceros auklet (*Cerorhinca monocerata*) and sooty shearwater (*Puffinus griseus*); and the marine mammals harbor porpoise (*Phocoena phocoena*) and the California sea lion (*Zalophus californianus*). Management of *L. opalescens* stocks therefore extends beyond fisheries interests alone; it must also take into account the role of this species in the ecology of California coastal waters.

LIFE HISTORY OF *LOLIGO OPALESCENS*

Loligo opalescens is a nearshore loliginid squid that inhabits continental shelf waters off the west coast of North America. A key feature of its life cycle is the spawning

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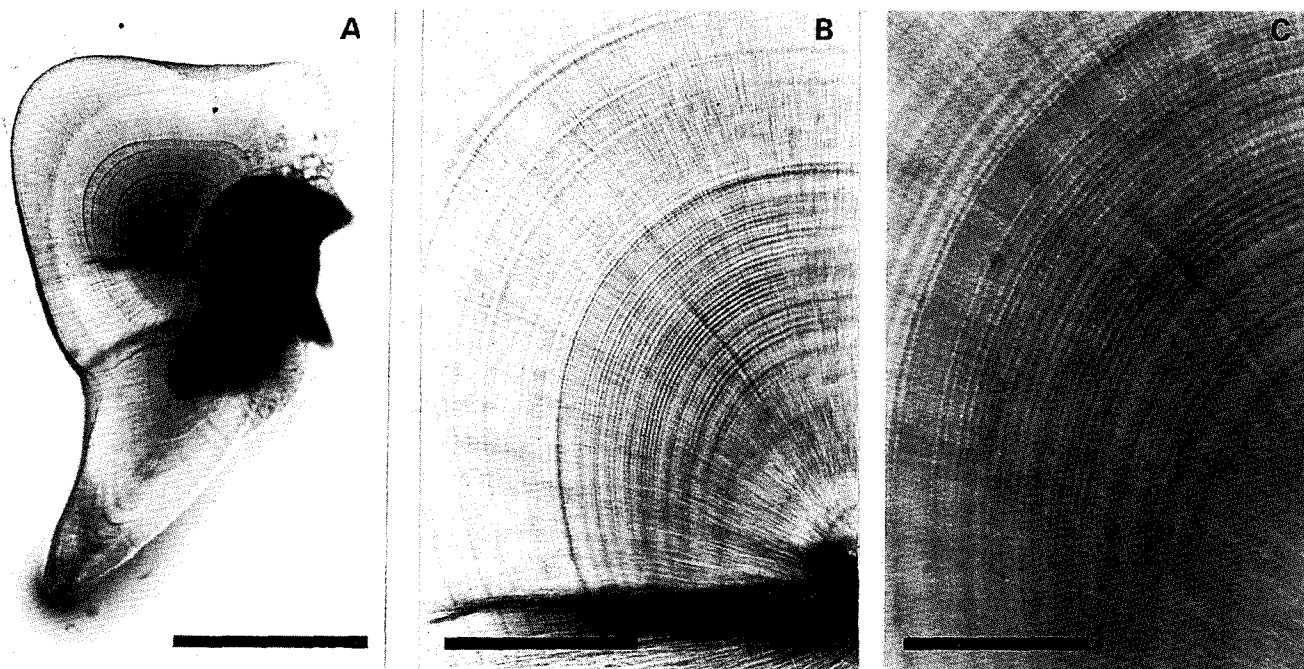


Figure 1. The ground and polished statolith of a female *Loligo opalescens* (128 mm mantle length, age 311 d; see Jackson 1994b) captured off central California in 1990: A, whole statolith (scale bar = 500 μm); B, close-up of lateral region showing detail of increment structure (scale bar = 100 μm); C, close-up of individual increments in the lateral region (scale bar = 50 μm).

aggregation which takes place in relatively shallow waters off California. Before reproducing, squid appear to be more dispersed, with some individuals in deeper water. For spawning, they form huge aggregations and produce benthic egg masses that can be up to 12 m in diameter and over a meter in depth (Hixon 1983).

This species appears to be a true terminal spawner, with death following soon after spawning. Analysis of the reproductive system of males (Grieb and Beeman 1978) and females (Knipe and Beeman 1978) revealed that the maturation process is terminal; there is no sign of renewal of the gametogenic process in males and no stage I preoocytes in females. There is also a dramatic emaciation of the mantle tissue in association with maturation; its thickness decreases approximately 24% in males and 42% in females (Fields 1965, cited in Hixon 1983).

AGE AND GROWTH

Growth estimates for *L. opalescens* have come from length-frequency analysis, culture data, and limited use of age information. Fields (1965, cited in Hixon 1983) used length-frequency analysis in an early attempt to understand growth. These early results suggested a growth rate of 4 mm/month and a life span of about two years.

Knowledge of squid biology has been greatly enhanced with the discovery of daily statolith increments. There is a growing body of information on growth and life spans of squids based on data obtained from statoliths (Rodhouse and Hatfield 1990; Jackson 1994a). The daily

periodicity in production of statolith increments has been validated in a number of species (Jackson 1994a; Jackson et al. 1997). Statolith analysis reveals information on hatch date, individual age, and average growth rates (fig. 1). Analysis of the width of daily rings may also provide information on daily growth. There is now the potential for using the squid gladius to analyze specific daily growth rate (Arkhipkin and Bizikov 1991; Bizikov 1991; Jackson et al. 1993; Bizikov 1995; Perez et al. 1996).

Spratt (1978) highlighted the significance of increments within the statoliths of *L. opalescens* when statolith analysis was in its infancy. Although Spratt identified what he thought were daily increments within the dorsal dome of the statolith, he also suggested that more prominent increments were produced monthly. Enumeration of these daily as well as "monthly" increments also indicated a life span of almost two years.

Culture of *L. opalescens* provided another avenue to understanding growth parameters and life span. Work by Yang et al. (1983, 1986) resulted in a radically different form of growth. Cultured individuals could be modeled by an exponential equation, and maturity was reached in captivity in less than 200 d, with spawning taking place between 196 and 239 d. Culture work yielded considerably different life-span estimates for *L. opalescens* than previous fieldwork, which suggested a life span of about two years (fig. 2).

A second preliminary analysis of statolith growth increments was undertaken by Jackson (1994b), who aged

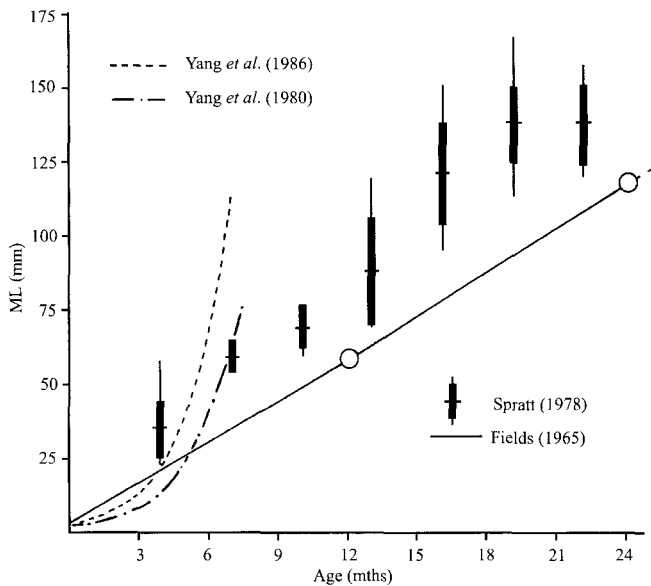


Figure 2. Summary of growth models developed for *Loligo opalescens* (modified from Hixon 1983).

12 individuals of *L. opalescens* captured off Monterey, in central California. This analysis interpreted all increments as daily, in contrast to earlier work by Spratt (1978). The good agreement in the results of Jackson (1994b) and Yang et al. (1986) suggests that *L. opalescens* may complete its life in less than a year off central California (fig. 3).

Such studies underscore the significance and validity of ageing studies for understanding squid growth, and further reveal the inadequacies of applying length-frequency analysis to squid.

INFORMATION FROM OTHER LOLIGINID POPULATIONS

An examination of age and growth parameters from other loliginid populations can provide general features of age and growth of loliginids. Statolith ageing techniques have now been applied to a number of loliginid populations around the world (table 1). The results reveal that loliginid life spans are generally short; only several species live longer than a year, and all species complete their life cycles in fewer than 18 months. *Loligo vulgaris reynaudii* appears to have one of the longest life spans; some large males may live longer than 15 months (Lipinski 1991; Augustyn et al. 1994). Generally, temperate species complete their life cycle in about a year; tropical species can complete their life cycle in <200 d; and very small tropical species such as *Loliolus noctiluca* can reach maturity in 3 months or less and complete their life cycle in 4 months (Jackson and Choat 1992).

Loliginid squids show a marked response to environmental temperature changes because of their short lives

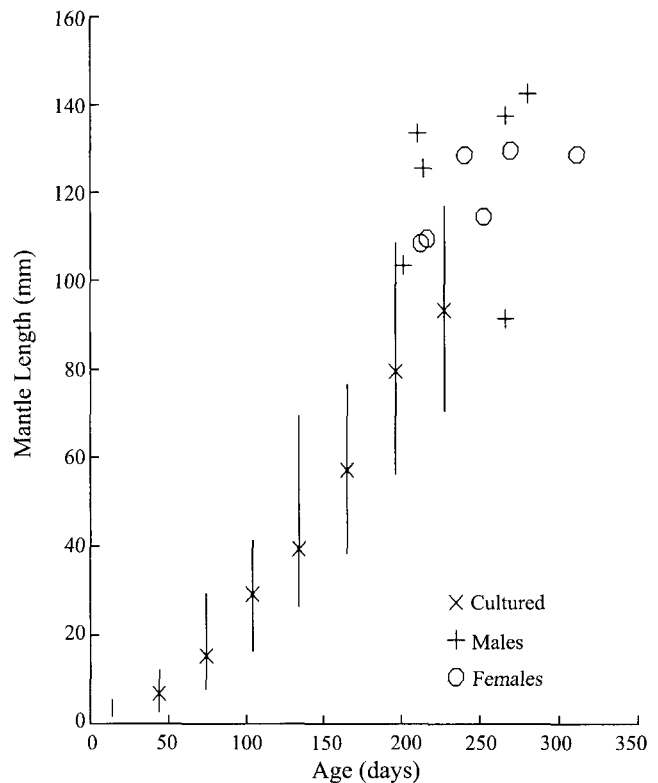


Figure 3. Age estimates for field-captured individuals of *Loligo opalescens* compared to data generated for this species raised in captivity (from Jackson 1994b).

(e.g., Forsythe 1993). Age analysis of field-caught individuals (Jackson and Choat 1992) revealed seasonal variation in growth in the tropical loliginid *Photololigo* sp. (referred to as *Loligo chinensis*, but now known to be a new species; see Yeatman and Benzie 1993, 1994), which completed its life span in 115 d in summer but lived longer than 170 d in winter. These differences in growth rates also affected seasonal maturation rates in the species (Jackson 1993).

Ageing work on *Loligo gahi* (Hatfield 1991) and *Loligo pealei* (Brodziak and Macy 1996) also showed that individuals which hatched in different months had different growth rates. Recent work on *Loliguncula brevis* (Jackson et al. 1997) revealed that small, shallow-water loliginids can exhibit marked seasonal differences in growth as a result of pronounced seasonal temperature fluctuations. The age of this species can range from 81 to 172 d, depending on the prevailing temperatures during growth (especially during the early growth period).

Seasonal growth variation is so important that ageing individuals without a knowledge of their past life history would make it virtually impossible to understand the form of growth. For example, figure 4a shows all the age data for *Loliguncula brevis* from Jackson et al. (1997). Presenting this data without a knowledge of the season of capture can mask the form of growth. The scatter-

TABLE 1
 Size and Age Data from Different Loliginid Populations around the World, on the Basis of Statolith Age Analysis

Region	Species	Age (days)	Mantle length (mm) ^a	Environment	Reference
North America	<i>Loligo opalescens</i>	280	142	Temperate	Jackson 1994b
	<i>Loligo pealei</i>	296	303–440	Temperate	Macy 1995
	<i>Lolliguncula brevis</i>	172 summer 95 winter 81 autumn	72 71 82	Warm temperate	Jackson et al. 1997
South America	<i>Loligo gahi</i>	439	210–350	Temperate	Hatfield 1991
Europe	<i>Loligo forbesi</i>	377 male 359 female	431 263	Temperate	Collins et al. 1995
	<i>Loligo vulgaris</i>	~245	~274 (not full size range)	Warm temperate	Natsukari & Komine 1992
North Africa	<i>Loligo vulgaris</i>	396 male 335 female	498 290	Tropical	Arkhipkin 1995
	<i>Alloteuthis africana</i>	208 male 187 female	205 155	Tropical	Arkhipkin & Nekludova 1993
	<i>Alloteuthis subulata</i>	231 male 172 female	135 72	Tropical	Arkhipkin & Nekludova 1993
South Africa	<i>Loligo vulgaris reynaudii</i>	~540	360	Temperate	Lipinski 1991
Japan	<i>Photololigo edulis</i>	350	~404	Warm temperate	Natsukari et al. 1988
	<i>Heterololigo bleekeri</i>	385.5 male 336.5 female	320 210	Warm temperate	Kinoshita 1989
Thailand	<i>Loligo chinensis</i>	172 male 151 female	271 235	Tropical	Chotiyaputta 1997
	<i>Loligo duvauceli</i>	98 male 95 female	119 110	Tropical	Chotiyaputta 1997
	<i>Sepioteuthis lessoniana</i>	188	184	Tropical	Jackson 1990a
Australia	<i>Photololigo</i> sp. ^b	173 winter 115 summer ~102	167 167 ~92	Tropical Tropical	Jackson & Choat 1992
	<i>Photololigo</i> sp. 1	157	115	Tropical	Moltschaniwskyj 1995
	<i>Loliolus noctiluca</i>	112	90	Tropical	Jackson & Yeatman 1996
				Tropical	Jackson & Choat 1992

Age and mantle length values were generally provided in the reference or estimated from size-at-age plots included in it.

^aThe data refer to sizes of oldest individuals, which do not necessarily indicate the maximum obtainable size for each species.

^bThis species was referred to as *Loligo chinensis* in Jackson and Choat 1992. It is now known to be a new, undescribed species of *Photololigo* (see Yeatman and Benzie 1993, 1994).

plot in figure 4a suggests that *L. brevis* might have asymptotic growth, with a slowing after about 100 d, and a life span of about 170 d. However, when the data are plotted with the appropriate seasonal segregation (fig. 4b) it becomes apparent that growth is nonasymptotic; squids that hatched during warmer seasons had faster growth rates and shorter lives.

Results of ageing work on squid suggest that growth is continuous, nonasymptotic, and exponential or linear in form. In many species, growth of the gonad appears to coincide with growth of the soma. We currently do not fully understand all the physiological processes governing how squid grow. They do, however, appear to grow in a fundamentally different way than fish (e.g., O'Dor and Webber 1986; Alford and Jackson 1993). Moltschaniwskyj (1994) has provided a physical mechanism for the observed differences in the form of growth between squid and fish. Fish appear to grow initially by recruitment of new muscle fibers (hyperplasia) and with an increase in muscle fiber diameter (hypertrophy). Their final size may be influenced by the number of muscle fibers present once hyperplasia ceases, and individuals with more muscle fibers have the potential to reach a

larger size (Moltschaniwskyj 1994). Squid also show both mechanisms of muscle fiber growth, but with the fundamental difference that hyperplasia does not cease; rather, recruitment of new muscle fibers is a continuous process throughout life. This phenomenon has also recently been documented for *L. opalescens* (Preuss et al. 1997).

FUTURE RESEARCH

Growth and Reproduction

The growth of *L. opalescens* is still poorly understood. Because of its wide latitudinal distribution, this species encounters considerable temperature differences. It is therefore likely to exhibit marked plasticity in growth as a result of varying water temperatures. Growth may also differ depending on the season of hatching or other physical phenomena such as El Niño events.

There appears to be a continuum in squid reproductive strategies, from species that are multiple (or batch) spawners (e.g., *Stenoteuthis oualaniensis*, Harman et al. 1989; *Loligo forbesi*, Boyle et al. 1995) to true terminal spawners that die in association with or soon after spawning (e.g., *L. opalescens*, Grieb and Beeman 1978; Knipe

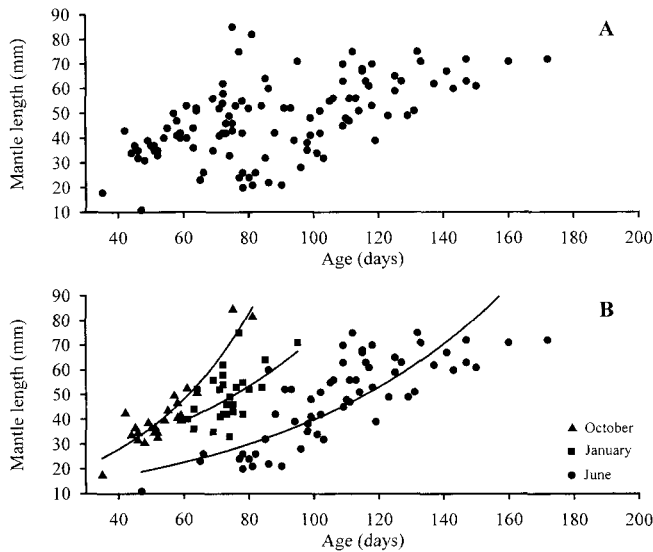


Figure 4. Size-at-age data for *Loliguncula brevis* from the Gulf of Mexico (Jackson et al. 1997). A, The scatterplot resulting from pooling all individuals, with the data suggesting a possible asymptotic growth curve; B, the same scatterplot showing the month of collection and the associated exponential growth curves. Note that neither the x nor the y axis starts at zero.

and Beeman 1978; *Moroteuthis ingens*, Jackson and Mladenov 1994). The physical processes of terminal spawning in *L. opalescens* need to be described in more detail. The deepwater squid *M. ingens* was shown to undergo a dramatic tissue breakdown process in association with maturation and spawning that results in the loss of virtually all mantle musculature, leaving only a collagen matrix. The loss of mantle thickness in *L. opalescens* (Fields 1965, cited in Hixon 1983) may be due to a similar process.

Potential Research Protocols

Although there are some historical data on the biology of *L. opalescens*, there is an urgent need to establish biological parameters for this species. Such life-history data can then be used to develop necessary management models. The following studies would greatly facilitate our understanding of *L. opalescens* biology.

1. Obtain information on age, growth, maturation rates, and life span from analysis of statolith increments. Statoliths are the tools of choice for determining the basic demographic parameters needed for population management. Since *L. opalescens* covers such a large latitudinal range (Alaska to Mexico, Hixon 1983), samples should be taken from a variety of sites covering as large a latitudinal range as possible. This will document the geographic variability in growth rates. Sampling effort should also be conducted year-round, and should span several years from one or more key sites to document differences in growth rates, maturation rates, and life spans of different seasonal cohorts.

2. Validation experiments should be undertaken to document the periodicity of statolith increments. This would involve staining live squid with either tetracycline or calcein (e.g., Jackson 1989, 1990a, b) and maintaining individuals in captivity to verify the one-ring:one-day hypothesis. Alternatively, other techniques such as analysis of marginal increments for individuals captured over a 24 hr period may be possible (Jackson 1994a).
3. Studies into squid condition in association with maturation should be undertaken to describe the dynamics of mantle muscle in association with terminal spawning. If a process of tissue degradation occurs in *L. opalescens* similar to that in *M. ingens*, then females nearing the end of their lives may have very little muscle tissue left.
4. Examine the possibility of using predators as sampling devices. Squid are notoriously difficult to sample, especially the younger stages. But some species such as the curlfin turbot may prove to be excellent sampling devices for juvenile squid. Croxall and Prince (1996) have highlighted the usefulness of seabirds for sampling squids. Some species such as the rhinoceros auklet may also be an effective sampling tool. Species that prey on younger stages may offer a valuable means for sampling the relative abundance of juvenile squid in order to predict future recruitment into the adult population. Alternatively, periodic collections of scats or vomits of the California sea lion may offer an effective way to monitor the population structure of squid in a specific region. Such analysis is especially effective because specific squid species can be identified by undigested beaks (e.g., Klages 1996), and beak size can be related to squid size (Clarke 1986). Examining such remains should make it possible to reconstruct size frequencies of squid.
5. Radio acoustic positioning and telemetry (RAPT) offers one means of obtaining information on movements of individuals within a spawning region over small scales of hundreds of meters to several kilometers (e.g., Sauer et al. 1997). Individual squid can be tracked over longer distances with telemetry (e.g., Nakamura 1991) to obtain information on longer migrations or movements into deeper water offshore. Traditional tagging methods (Nagasawa et al. 1993; Takami and Suzuuchi 1993) may also be useful for obtaining information on long-distance migrations along the California coast.
6. Light trapping (Moltschaniwskyj and Doherty 1995) may be a technique for monitoring the abundance and distribution of juvenile squid within the water column.

CONCLUSION

California management agencies are in a unique position to collect basic biological data on *L. opalescens* before fishing pressure increases. As the fishery progresses, ongoing monitoring and assessment will provide basic biological information that can serve as a basis for developing management strategies. We still do not fully understand the importance of *L. opalescens* off the North American coastline. Continued research with a variety of techniques will help to answer important biological questions that are now being asked. Such focused research will also serve ecological and conservation needs because the resulting data will help to clarify the role that *L. opalescens* plays in the California coastal food web.

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