

REVISED BIOLOGY AND MANAGEMENT OF LONG-FINNED SQUID (*LOLIGO PEALEI*) IN THE NORTHWEST ATLANTIC

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ABSTRACT

New biological information on the growth and life cycle of the long-finned squid (*Loligo pealei*) became available as ageing procedures based on statoliths were applied to this valuable commercial resource in the 1990s. It was found that *L. pealei* grew very rapidly and completed its life cycle in less than one year. This research led to several important changes in management for the *L. pealei* fishery. First, biological reference points were developed for summer- and winter-hatched squid based on differences in growth and maturation rates between seasonal cohorts. Second, a precautionary approach was taken toward determining the annual allowable catch and long-term potential yield. The revised estimate of long-term potential yield of 21,000 metric tons (t) based on a life span of less than one year was less than half of the previous estimate of 44,000 t, which was based on an assumed life span of roughly two years. Third, limited entry was applied to the commercial squid fishery because the stock was fully exploited on the basis of the revised estimate of long-term potential yield. The Mid-Atlantic Fishery Management Council has set the current annual domestic allowable harvest of *L. pealei* to equal the revised estimate of long-term potential yield, and in-season monitoring of landings and enforcement of the domestic allowable harvest level have been planned.

INTRODUCTION

The long-finned squid (*Loligo pealei*) ranges from the Gulf of Venezuela, Venezuela (Summers 1983), to Newfoundland, Canada (Dawe et al. 1990). The *L. pealei* resource in the northwest Atlantic is distributed from its southern zoogeographic boundary of Cape Hatteras, North Carolina, to Georges Bank (NEFSC 1996). Although separate populations of *L. pealei* exist in the Gulf of Mexico (Hixon 1980) and along the Eastern Scotian Shelf (Dawe et al. 1990), these portions of the resource have not been subject to intensive commercial harvest and are outside the scope of this study.

North of Cape Hatteras, the *L. pealei* population undertakes seasonal migrations to avoid cold waters with bottom temperature lower than 8°C (Summers 1969;

Serchuk and Rathjen 1974; Vovk 1978; Lange and Sissenwine 1983) and to occupy favorable spawning grounds close to juvenile nursery areas in coastal waters (Vecchione 1981). In early winter *L. pealei* migrate offshore to avoid the autumn cooling of coastal waters. Submarine canyons and areas along the edge of the continental shelf at depths of 100–250 m have warmer water temperatures during winter (9°–12°C) and provide suitable habitat for *L. pealei* (Vovk 1978; Lange and Sissenwine 1983; Summers 1983). During spring, *L. pealei* migrate inshore to continental shelf and coastal waters (<100 m), where they spawn and feed. In general, these migrations can complicate interpretation of length-frequency data and bias estimates of squid growth that are based on localized sampling (Hatfield and Rodhouse 1994).

Diel migrations can also complicate the interpretation of *L. pealei* catch and length-frequency data. Although adult *L. pealei* are primarily demersal (cf. Hanlon et al. 1983), juvenile *L. pealei* migrate vertically upward in the water column at night to avoid predation or to acquire prey (Summers 1968; Brodziak and Macy 1996). As a result of these movements, bottom trawl catches of *L. pealei* juveniles and adults are generally larger during daylight hours, and estimates of the relative magnitude of diel effects on research survey catches of *L. pealei* have been developed (Sissenwine and Bowman 1978; Brodziak and Hendrickson, in press).

New biological information on the growth and life cycle of *L. pealei* became available as ageing procedures based on statoliths were applied to this valuable commercial resource in the 1990s (Macy 1995a). Results showed that *L. pealei* grew very rapidly and completed its life cycle in less than one year (Macy 1995a; Brodziak and Macy 1996). This research led to several important changes in management for the *L. pealei* fishery.

In this paper, I describe how fishery management procedures for the *L. pealei* resource in the northwest Atlantic were revised to account for improved understanding of its life cycle and growth. I begin by describing some previous theories on the life cycle and growth of *L. pealei*. The history of fishery management of this loliginid is also briefly discussed. I then describe the application of statolith ageing techniques to *L. pealei* and identify some important consequences of this research. Revised management measures for the *L. pealei* fishery and their

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rationale are described; these measures include revised biological reference points, estimates of long-term potential yield, and limited entry to the commercial fishery. Last, some areas of future research that may reduce uncertainty in the management of the *L. pealei* resource are discussed.

EARLY IDEAS ABOUT LIFE CYCLE AND GROWTH

Previous researchers assumed that the life span of *L. pealei* exceeded one year (Verrill 1881; Mesnil 1977; Lange and Sissenwine 1983; Summers 1983; NEFSC 1988). Length-frequency data collected from research surveys and other sources generally indicated the presence of multiple cohorts within a year due to a protracted spawning season. But these data also suggested that there were two primary cohorts each year: spring and late summer (Summers 1968, 1971; Mesnil 1977; Lange 1981; Lange and Sissenwine 1983). Analysis of the modes of successive length-frequency samples led to the hypothesis that these two primary cohorts were linked through time (Mesnil 1977; Summers 1983; Lange and Sissenwine 1983).

In the crossover life-cycle model of Mesnil (1977), the spring cohort was expected to return to spawn in late summer of the following year at an age of about 14–16 months. The late-summer cohort was expected to return to spawn in spring two years later at an age of about 20–22 months. Thus the two primary cohorts produced each year were expected to maintain separate breeding lines that successively changed from a spring spawner life cycle to a late-summer spawner life cycle. This was called the crossover life-cycle model and was accepted as the best hypothesis for *L. pealei* until the application of statolith ageing to this species in the 1990s (Brodziak and Macy 1996).

Historically, research on the pattern and rate of growth of *L. pealei* was based on analysis of the progression of modes within successive length-frequency samples (Verrill 1881; Summers 1968, 1971; Cohen 1976; Mesnil 1977; Lange 1980; Lange and Sissenwine 1980; Macy 1980; Hixon et al. 1981). These analyses suggested growth rates of 10–24 mm of mantle length per month (Hixon et al. 1981).

The assumption that growth of *L. pealei* followed a Von Bertalanffy growth curve was used to analyze some inferred length-at-age data (Ikeda and Nagasaki 1975; Lange 1980), where cohort ages were inferred from modes of length-frequency distributions. However, this asymptotic growth model did not seem appropriate for some of the inferred length-at-age data (Lange 1980; Lange and Sissenwine 1983).

Regardless, alternative indirect estimates of growth have been used to calculate yield per recruit for various fishery selectivity patterns. When coupled with estimates

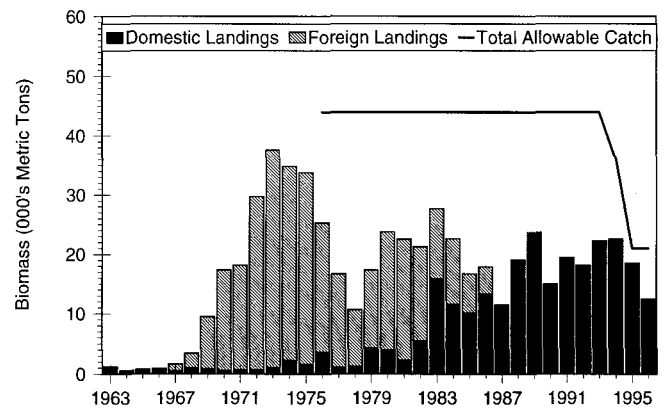


Figure 1. Foreign and domestic landings of *Loligo pealei* from Cape Hatteras to the Gulf of Maine, 1963–96, and total allowable catch.

of recruitment, these yield-per-recruit estimates provided a rationale for evaluating the potential yield from the *L. pealei* resource under various fishery selectivity patterns and fishing mortality rates (Lange 1981; Lange and Sissenwine 1983).

HISTORY OF FISHERY MANAGEMENT

Before the 1960s, domestic fisheries for *L. pealei* were small-scale, and much of the yield was used as bait. Fleets from Japan, Spain, and the USSR began harvesting the *L. pealei* resource during the late 1960s in offshore waters of New England and the Mid-Atlantic Bight (Lange and Sissenwine 1983). These trawl fisheries were primarily prosecuted in winter, when squid were aggregated near canyons or along the edge of the continental shelf. Eventually, the foreign fisheries were managed on a total allowable catch basis under the auspices of the International Commission for the Northwest Atlantic Fisheries (ICNAF). An initial total allowable catch (TAC) of 71,000 t was established for combined landings of *L. pealei* and northern shortfin squid (*Illex illecebrosus*) in 1974–75 (Lange and Sissenwine 1980); a separate TAC for *L. pealei* was set at 44,000 t in 1976–77. However, the United States withdrew from ICNAF after passage of the U.S. Fishery Conservation and Management Act (FCMA) of 1976, which established national responsibility for fishery resources within 200 miles of U.S. land boundaries. As a result, total landings of *L. pealei* by foreign nations were reduced through the late 1970s and early 1980s as domestic fishers supplanted foreign fishers under auspices of the FCMA (fig. 1). Foreign fishing for *L. pealei* ceased in 1987.

The traditional fishing season for *L. pealei* by domestic fishers extended from late spring through summer, when squid were available inshore (Lange et al. 1984; Brodziak and Rosenberg 1993). Many vessels in the domestic fishery used bottom otter trawl gear to capture squid, although some landings were made inshore

with floating traps and fish weirs (McKiernan and Pierce 1995). In the early 1980s, however, the domestic trawl fleet began to expand and to harvest more squid offshore during winter. Most vessels in the winter offshore fishery were stern trawlers (150–2,000 gross registered tons) that harvested *L. pealei* on its overwintering area along the edge of the continental shelf at depths of 100–500 m (Lange and Sissenwine 1983). As a result, the domestic fishery now has two components: an inshore summer fishery and an offshore winter fishery (NEFSC 1996). The development of a domestic winter fishery had important consequences for the management of the *L. pealei* resource because it led to an expansion of domestic fishing effort directed at this species.

STATOLITH AGEING

Squid statoliths are paired calcareous structures that are functionally analogous to fish otoliths (Rodhouse and Hatfield 1990). Fine, ringlike structures within statoliths were observed by Clarke (1966), who suggested that these increments might provide information on squid age. But it was not until the early 1990s that statolith ageing became an accepted method for measuring squid age (Jereb et al. 1991; Jackson et al. 1993; Jackson 1994a). Growth increments in the statolith appear as pairs of light and dark bands formed over a 24-hour period (Jackson 1994a). These increments have been shown to be formed on a daily basis for several squid species (Hurley et al. 1985; Lipinski 1986; Jackson 1990a, b, 1994b; Jackson et al. 1993).

Macy (1995a) applied statolith ageing techniques to *L. pealei* in the early 1990s. Statolith ageing of this species was difficult because of the fine scale of increment structure; as a result, Macy used digital image analysis to improve the resolution of the fine increments. This research indicated that the largest specimens (over 40 cm long) were less than 300 days old (Macy 1995a; Brodziak and Macy 1996). Verification of the one-day one-increment hypothesis was difficult for *L. pealei* because they can be challenging to rear in captivity (Summers 1983; Macy 1995a). Nonetheless, the hypothesis that statolith increments are formed daily in *L. pealei* is the most credible hypothesis on the basis of limited tetracycline marking data and by analogy with other loliginid species (Brodziak and Macy 1996).

The implications of statolith ageing research for squids have been substantial in recent years (Jackson 1994a). Patterns of growth for exploited species such as *L. pealei* appear to be linear or exponential, so that adult sizes do not approach an asymptote (Jackson 1994a; Brodziak and Macy 1996). This contrasts the asymptotic pattern of growth epitomized by the Von Bertalanffy growth curve, which is commonly used for analysis of size-at-age data for marine fishes.

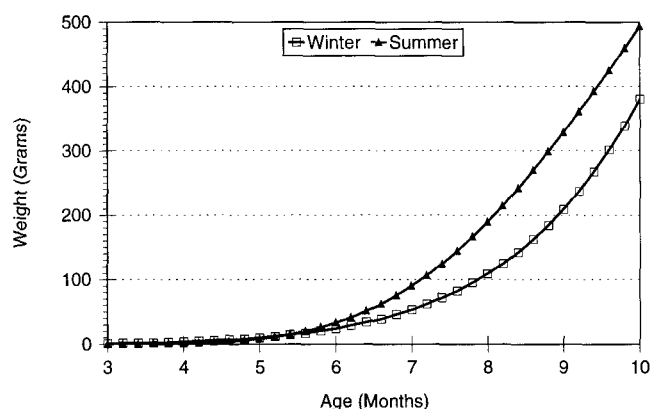


Figure 2. Size at age of winter-hatched (open square) and summer-hatched (solid triangle) *Loligo pealei*. (Data from Brodziak and Macy 1996.)

In part, the acceptance of statolith ageing techniques as valid measures of age has led to the realization that squids, such as *L. pealei*, grow more rapidly than once thought and do not conform to commonly accepted growth models for finfish. Although there is still some debate over the general pattern of growth of squids, the examination of nonasymptotic growth curves is recommended, and objective approaches to determine the most parsimonious growth model have been developed (Brodziak and Macy 1996). For *L. pealei*, the statolith ageing research led to revised estimates of key life-history parameters and to improved interpretations of abundance measures and fishery impact (Brodziak and Macy 1996; NEFSC 1996).

Revised Life-History Parameters

Revised estimates of life-history parameters of *L. pealei* are reported in Brodziak and Macy 1996 and NEFSC 1996. Revised estimates of growth of *L. pealei* in the northwest Atlantic were derived by Brodziak and Macy (1996). They found that seasonal differences in growth were substantial between squid hatched during “summer” (June–October) and “winter” (November–May). Weight at age increased exponentially for both summer- and winter-hatched squid, but growth was slower, on average, for winter-hatched squid, which experienced lower temperatures as juveniles (fig. 2). The slower growth of winter-hatched squid implied that the yield per recruit would differ for the domestic winter fishery, which primarily captured summer-hatched squid, in comparison to the domestic summer fishery, which primarily harvested winter-hatched squid.

Revised monthly estimates of the instantaneous natural mortality rate of *L. pealei* were derived with the new information on life span. Three methods were used to estimate natural mortality (NEFSC 1996). On the basis of Hoenig’s regression method (Hoenig 1983) and a maximal age of 296 days, instantaneous natural mortality was

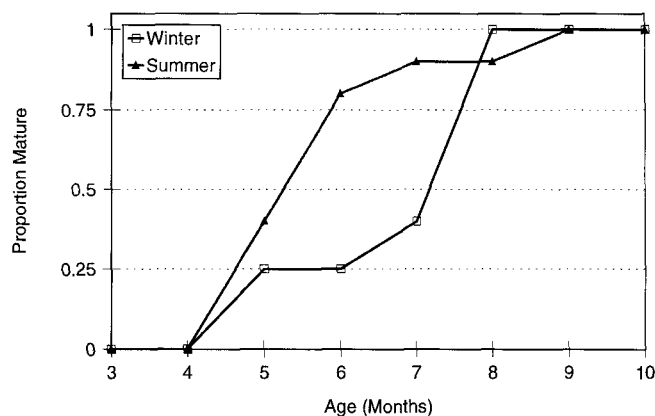


Figure 3. Fraction mature at age of winter-hatched (open square) and summer-hatched (solid triangle) *Loligo pealei*. (Data from Macy 1995b.)

estimated to be $M_m = 0.34$ per month. Another method was based on the analogy that the monthly natural mortality rate of *L. pealei* would be similar to that of other commercially exploited squid species. Rosenberg et al. (1990) reported a monthly natural mortality rate of $M_m = 0.26$ per month for *Illex argentinus*. The third method used the process of Peterson and Wroblewski (1984) to derive a natural mortality rate on the basis of animal size and bioenergetic constraints. With an assumed weight coefficient of growth of $k = 0.018$ per day estimated for female *L. pealei*, and a mean size of 25 g taken from the annual NEFSC autumn bottom trawl survey, it was estimated that monthly natural mortality was $M_m = 0.30$ per month. The average of these three estimates was $M_m = 0.3$ per month, and this value of natural mortality was accepted as the best current estimate for *L. pealei* (NEFSC 1996).

Revised estimates of fraction mature at age by hatch season were developed from statolith ageing and Macy's classification method for determining maturity stage of *L. pealei* (Macy 1982). The classification of squid as mature (stage III or IV) or immature (stage I or II) was accomplished for both summer- and winter-hatched *L. pealei* (NEFSC 1996). Empirical estimates of the fraction mature at age in months (Macy 1995b) were greater for summer-hatched *L. pealei* than for winter-hatched squid (fig. 3).

Interpretation of Abundance Measures and Fishery Impact

Research surveys conducted by the NEFSC during spring and autumn provide measures of *L. pealei* abundance and biomass (Lange and Sissenwine 1980, 1983; NEFSC 1996). These surveys have employed standard bottom trawl gear to sample demersal species composition and abundance on the continental shelf off the northeast United States from Cape Hatteras to the Gulf of Maine since the late 1960s (Azarovitz 1981). Both juve-

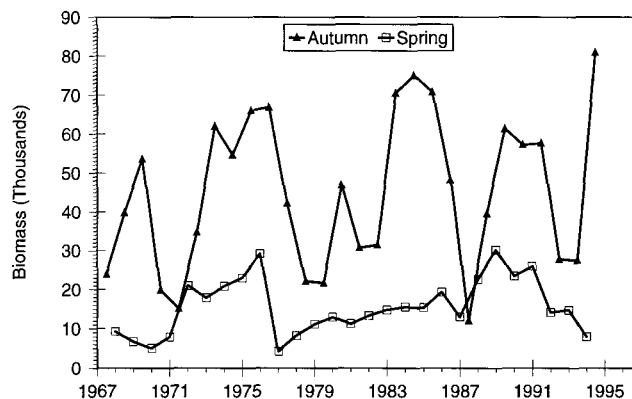


Figure 4. Diurnally adjusted swept-area estimates of *Loligo pealei* biomass (t) during autumn (solid triangle) and spring (open square) NEFSC bottom trawl surveys, 1967-94.

nile and adult *L. pealei* have been routinely captured during the NEFSC spring and autumn bottom trawl surveys since these surveys began in the 1960s. Trends in abundance of *L. pealei* during research surveys were difficult to interpret under the crossover life-cycle model because the expected life span of about two years suggested that there would be more moderate changes in population size over several years than were observed. In contrast, under the annual life-cycle model of *L. pealei*, short-term patterns of above-average or below-average abundance can be observed from the spring and autumn survey series (fig. 4). These patterns are due to the approximate 6-month lag between hatching and recruitment to the sampling gear (Brodziak and Macy 1996, fig. 3).

RESEARCH SURVEYS

Measures of the abundance of the *L. pealei* population north of Cape Hatteras have been developed from the NEFSC spring and autumn bottom trawl surveys on the basis of diurnally adjusted swept-area estimates of biomass (Lange and Sissenwine 1980, 1983; NEFSC 1996). In general, the catchability of *L. pealei* by the bottom trawl survey gear is lower at night than during the day, although the diel effect is more pronounced for juveniles than for adults (Brodziak and Hendrickson, in press). Size-specific correction factors have been developed to adjust nighttime catches of juvenile and adult squid to equivalent daytime units (Sissenwine and Bowman 1978; NEFSC 1996; Brodziak and Hendrickson, in press). For *L. pealei*, the application of correction factors for diurnal catchability leads to a time series of diurnally adjusted swept-area biomass estimates (fig. 4). The diurnally adjusted spring biomass estimate provides an estimate of population biomass at the beginning of the domestic summer fishery (April-September). Similarly, the diurnally adjusted autumn biomass estimate provides a measure of population biomass at the beginning of the winter fishery (October-March).

COMMERCIAL FISHERY

Estimates of standardized landings per unit of effort have been developed for winter and summer bottom otter trawl fisheries that capture *L. pealei* (NEFSC 1996). Here the winter fishery is defined as bottom otter trawl fishing trips during October through March with at least 10% landings of *L. pealei* by weight. Thus, the winter fishery is a contiguous 6-month period that includes fishing trips from October through December of the previous year. The summer fishery is defined similarly, as bottom otter trawl fishing trips during April through September with at least 10% landings of *L. pealei* by weight.

Estimates of standardized landings per unit of effort (LPUE) and standardized fishing effort were derived for both the winter and summer fishery with a general linear model with main effects of year, tonnage class, area, and month. The winter fishery shows increasing trends in LPUE and fishing effort during 1983–93 (fig. 5). In contrast, the summer fishery shows a declining trend in LPUE during 1983–93 and a moderate decline in effort during 1986–93 (fig. 6). When winter fishing effort is compared to LPUE the following summer, there

is a significant decreasing trend in summer LPUE with increasing winter effort (fig. 7). Although this trend does not imply causation, since environmental factors may be involved, it does suggest the possibility that high levels of winter fishing effort may have reduced recruitment to the subsequent summer fishery.

Estimates of monthly fishing mortality rates for winter and summer fisheries have also been developed from diurnally adjusted estimates of spring and autumn abundance and fishery landings. In particular, swept-area biomass from the spring survey provides an estimate of population size at the beginning of the summer fishery, whereas biomass from the autumn survey provides an estimate of population size at the beginning of the winter fishery. Estimates of 6-month exploitation rates were obtained by dividing winter or summer fishery landings by estimated population biomass at the beginning of the fishery season. The 6-month exploitation rates were converted to instantaneous monthly rates for comparison with biological reference points (fig. 8). These mortality rates are based on landings and do not account for potential discarding of *L. pealei* in the trawl fisheries.

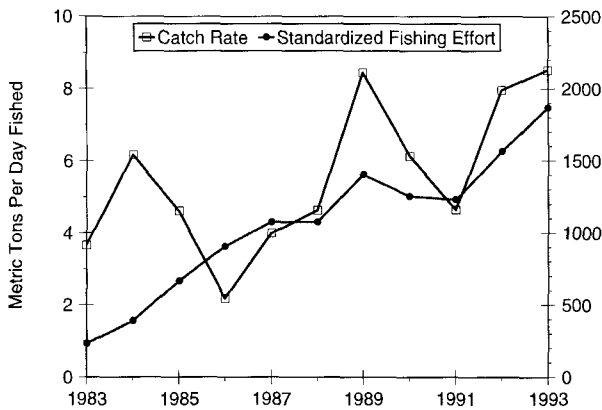


Figure 5. Standardized catch rate (open square) and fishing effort (solid circle) for the domestic winter trawl fishery, 1983–93.

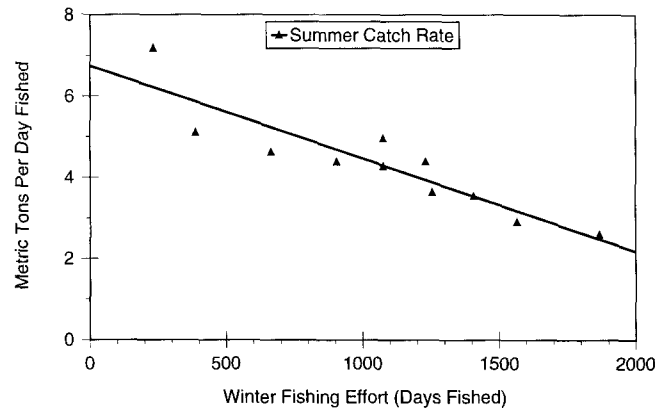


Figure 7. Standardized fishing effort in the winter trawl fishery versus standardized catch rate in the subsequent summer trawl fishery, 1983–93.

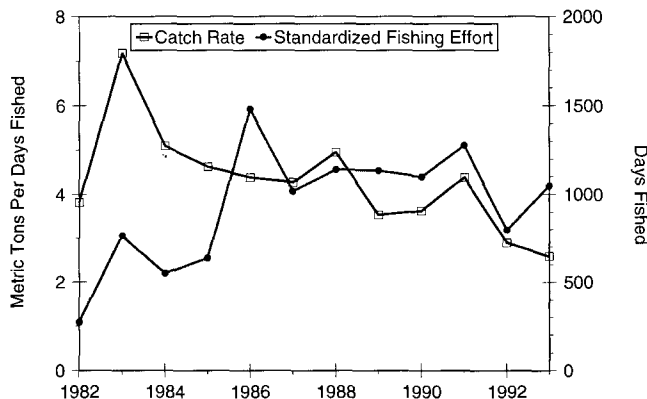


Figure 6. Standardized catch rate (open square) and fishing effort (solid circle) for the domestic summer trawl fishery, 1982–93.

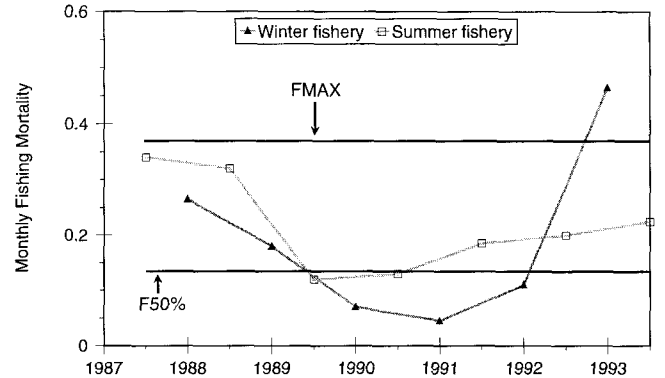


Figure 8. Monthly estimates of fishing mortality in the winter (major tick mark) and summer (minor tick mark) trawl fisheries in comparison to target (F50%) and overfishing (FMAX) fishing mortality rates, 1987–93.

REVISED MANAGEMENT MEASURES

Management measures for the *L. pealei* resource were revised to account for the improved understanding of its life cycle and life-history parameters (Brodziak and Macy 1996; NEFSC 1996). The revisions included changes in biological reference points defining overfishing and target harvest rates, determination of long-term potential yield, and provisions for limited entry to the fishery (MAFMC 1997).

Biological Reference Points

Biological reference points for *L. pealei* were revised to account for the improved estimates of life-history parameters. Of particular importance was revision of the former overfishing definition for *L. pealei*. This definition was based on a 3-year average of the relative abundance of juvenile *L. pealei* captured during the NEFSC autumn bottom trawl survey. In particular, the stock was considered to be recruitment overfished whenever the 3-year moving average of numbers of juvenile *L. pealei* (mantle length less than 9 cm) fell within the lowest quartile of the autumn juvenile time series. This overfishing definition was reviewed by a scientific panel and found to be a risky definition of overfishing for such a short-lived species (Rosenberg et al. 1994).

The fact that growth and maturation of *L. pealei* differed by hatch season complicated the development of biological reference points. Separate analyses of yield and spawning biomass per recruit were conducted for summer-hatched (June–October) and winter-hatched (November–May) cohorts to account for differences in size at age and fraction mature at age between seasonal cohorts (fig. 9). Standard methods to compute yield and spawning biomass per recruit were used (e.g., Gabriel et al. 1989). In these analyses, it was recognized that the winter and summer fisheries operated on a mixture of summer- and winter-hatched *L. pealei* and that the reference points would have to be interpreted cautiously if they differed substantially for summer- and winter-hatched cohorts.

An overfishing rate was defined on the basis of yield-per-recruit analyses for the summer- and winter-hatched *L. pealei*. The fishing mortality rate that maximized yield per recruit (FMAX) was chosen as the overfishing rate on the basis of yield-per-recruit considerations (Beverton and Holt 1957). Fishing in excess of the overfishing rate would result in growth overfishing of the stock. The estimated FMAX for winter-hatched squid was 0.38 per month; FMAX for summer-hatched squid was estimated to be 0.36 per month. The values of FMAX were virtually identical, although the realized yield per recruit at FMAX was higher for summer-hatched squid because of their more rapid growth. As a result, an overfishing

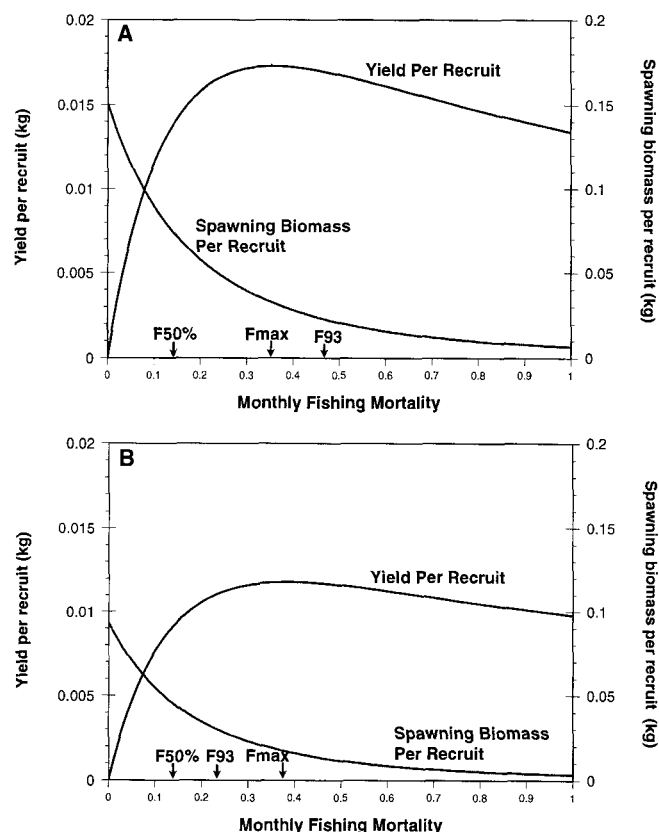


Figure 9. Yield and spawning biomass per recruit for (A) summer-hatched and (B) winter-hatched *Loligo pealei* as a function of monthly fishing mortality.

rate of FMAX was adopted for seasonal cohorts of the *L. pealei* stock.

Similarly, a target harvest rate was defined from analyses of spawning biomass per recruit for summer- and winter-hatched *L. pealei*. The target harvest rate was chosen to maintain average spawning potential of the *L. pealei* stock in the face of high natural mortality (0.3 per month); moderate fecundity on the order of 10,000 eggs per female (Summers 1971; Vovk 1972, cited in Summers 1983); and a complex mating system (Griswold and Prezioso 1981; Hanlon et al. 1997).

The target harvest rate for the *L. pealei* stock was chosen to be F50%, the fishing mortality rate that would maintain 50% of the maximum spawning potential of a cohort. The 50% level was selected on the basis of analogy with management of *Illex argentinus* in the Falkland Islands, where a proportional escapement goal of 40% determined the target exploitation rate. By analogy, if all *I. argentinus* were equal in their contribution to spawning potential, a proportional escapement goal of 40% would roughly correspond to F40% for a given cohort. The use of the more precautionary F50% level for *L. pealei* was considered reasonable because fecundity of *L. pealei* is roughly an order of magnitude lower than for *I. argentinus*.

It should be noted, however, that analyses of spawning biomass per recruit have generally not been conducted for management of squid resources. As a result, there were no comparative values of percent maximum spawning potential for squids that could be inferred to produce a sustainable target harvest rate. But in their review of how much spawning biomass per recruit could sustain fisheries resources, Mace and Sissenwine (1993) observed that many small pelagic fishery resources may require levels of 40%–60% of maximum spawning potential to maintain themselves. Given that *L. pealei* are subject to high natural mortality rates characteristic of small pelagic fishery resources, it was inferred that the high end (mean level plus two standard deviations) of percent maximum spawning potential reported for small clupeoid fish of roughly 50% (table 3 in Mace and Sissenwine 1993) would likely provide a precautionary level of spawning escapement for *L. pealei*.

The target harvest rate estimates of F50% for winter- and summer-hatched squid were 0.13 and 0.14 per month. Like the overfishing rate, the target harvest rate was virtually identical for both seasonal components. As a result, a target harvest rate of F50% was used for calculating long-term potential yield from two seasonal cohorts.

Long-Term Potential Yield

The annual long-term potential yield (LTPY) for the *L. pealei* resource in the northwest Atlantic was recalculated to account for the revised life-history parameters and improved understanding of the life cycle. The LTPY for the *L. pealei* stock was computed as the sum of the expected long-term potential yields for winter- and summer-hatched squid based on estimates of recruitment taken from the NEFSC spring and autumn surveys and the expected yield at the target harvest rate. Abundance of summer-hatched squid was measured during the autumn survey because they were primarily harvested in the winter fishery. Similarly, abundance of winter-hatched squid was measured during the spring survey because they were primarily harvested in the summer fishery.

Seasonal patterns of recruitment and growth were incorporated in the calculation of long-term potential yield from the *L. pealei* fishery. Estimates of *L. pealei* recruitment to the winter and summer fishing seasons were based on the diurnally adjusted swept-area estimates of total numbers of pre-recruits (squid less than 9 cm in mantle length) from the autumn and spring survey, respectively. Because of the rapid growth of *L. pealei*, all pre-recruits were assumed to be fully available to the commercial fishery during the 6 months following the survey. The expected LTPY for summer-hatched *L. pealei* (autumn pre-recruits) was computed as the average of the predicted yield for summer-hatched squid at the tar-

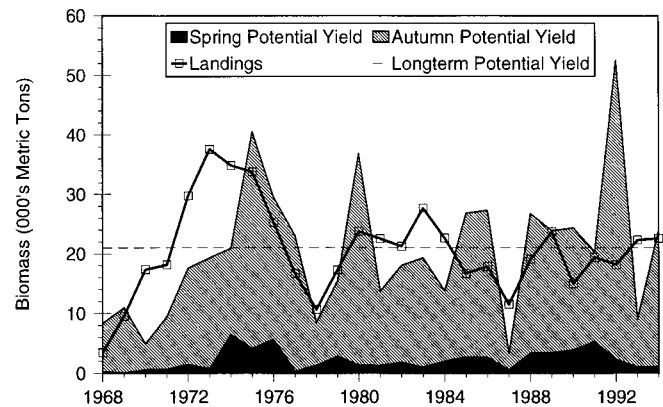


Figure 10. Potential yields of *Loligo pealei* from spring and autumn recruitment in comparison to annual landings (solid line) and long-term potential yield (dashed line), 1968–94.

get harvest rate of F50% times the estimated number of pre-recruits in the autumn survey for 1968–94. Similarly, the expected LTPY for winter-hatched *L. pealei* (spring pre-recruits) was computed as the average of the predicted yield for winter-hatched squid at F50% times the number of pre-recruits in the spring survey for 1968–94. As a result, the overall LTPY was estimated to be roughly 21,000 t, with 3,000 t (14%) coming from winter-hatched *L. pealei* and the balance (86%) from summer-hatched squid (fig. 10).

A precautionary approach was taken to determining LTPY because *L. pealei* are an important component of the northeast ecosystem as predators and prey. In this approach, LTPY was calculated on the basis of average levels of recruitment and the target harvest rate of F50%. This approach was precautionary in comparison to using FMAX as the optimum harvest rate to determine LTPY. Although the application of FMAX would produce the maximal yield per recruit attainable under the current exploitation pattern, this harvest rate would not ensure that spawning potential was maintained for this short-lived, semelparous species. If FMAX were used instead of F50%, the expected maximal yield for *L. pealei* would be about 26,000 t. Historically, landings in excess of 25,000 t have not been sustained by the *L. pealei* fishery because of fluctuations in abundance.

The revised estimate of long-term potential yield of 21,000 t on the basis of a life span of less than one year was less than half of the previous estimate of 44,000 t, which was based on an assumed life span of roughly two years (Lange and Sissenwine 1983). The Mid-Atlantic Fishery Management Council has set the current annual domestic allowable harvest of *L. pealei* to be equal to the revised estimate of long-term potential yield, and in-season monitoring of landings and enforcement of the domestic allowable harvest level have been planned.

Limited Entry

Provisions for limited entry to the *L. pealei* fishery were motivated by two primary considerations. First, the *L. pealei* stock was fully exploited on the basis of a scientific assessment of the resource and a consensus review of that assessment (NEFSC 1996). Because the stock was fully exploited, additional fishing effort directed at the stock would not be expected to increase fishery yields or net national benefits of harvesting the resource. Second, the potential for increased fishing effort on the *L. pealei* stock was substantial, given the amount of displaced fishing effort from the New England groundfish fishery and the increasing trend in winter trawl effort for *L. pealei* during 1983–93. Provisions of Amendment 7 to the Northeast Multispecies Fishery Management Plan were directed to limit fishing effort on New England groundfish stocks in the mid-1990s to reduce chronic overfishing and rebuild groundfish stocks. As a result of effort limitations on groundfish fishers, fishing effort formerly directed at groundfish could be expected to focus on *L. pealei*.

Development of limited-entry provisions for the *L. pealei* fishery was contentious, but permits were ultimately based on historic participation in the *L. pealei* fishery. In effect, vessels that participated in the *L. pealei* fishery during the 1980s or early 1990s were assigned limited-entry permits. This led to approximately 400 limited-entry permits for the *L. pealei* fishery (L. Hendrickson, NEFSC, Woods Hole, Mass., pers. comm.).

FUTURE RESEARCH

The recent application of statolith ageing techniques to *L. pealei* and other squid species has improved the understanding of squid life cycles and life-history parameters (Jackson 1994a). But there is much more research to do because, in comparison to marine finfish whose population dynamics have been studied for over a century (cf. Smith 1994), squids have not been as intensively investigated. Future research can reduce uncertainty and improve fishery management of *L. pealei* and other squid resources.

One primary area for future research is further investigation of the commercial fishery for *L. pealei*. Direct sampling of the age composition of landings and discards from the winter and summer fishery for *L. pealei* is essential to understanding the interaction between these fisheries. In particular, it will be useful to determine whether increased winter effort leads to reduced summer spawning, and whether low levels of summer spawning reduce the probability of high levels of recruitment to the winter fishery. The use of commercial fishery LPUE as a relative abundance index is another area for commercial fishery research. Further, the development of a dynamic assessment model that integrates commercial fishery and research survey data to estimate seasonal fish-

ing mortality rates and population abundance of *L. pealei* is an important topic for future research. Commercial fishery data may also provide more temporal and spatial detail on the seasonal distribution of *L. pealei*, and geostatistics and geographic information systems may have important application.

Another potential area of research is to quantify the importance of density-dependent effects on the population dynamics of *L. pealei* (Brodziak and Macy 1996). Little is known about the relation between spawning stock and recruitment for the *L. pealei* stock. It will be important to quantify the level of density-dependence in this relationship to refine understanding of the levels of spawning biomass needed for sustained resource productivity. Density-dependence as well as seasonal and annual variation in growth and maturation are important for informed management, but reducing uncertainties about these matters will require much more extensive age sampling than has been conducted to date.

Trophic dynamics and the effect of community-level interactions with *L. pealei* predators and competitors are also an important research topic. The northeast shelf ecosystem has undergone profound changes in species composition and abundance since the intensive foreign fisheries of the 1960s and 1970s (Sissenwine and Cohen 1991). How these changes have affected long-term productivity of *L. pealei*, a mid-trophic-level species, would be useful to quantify for management. The current management approach includes an implicit recognition of the importance of *L. pealei* as part of the ecosystem. In effect, the current estimate of long-term potential yield provides an upper bound on annual landings. Under this management approach, potential increases in yield due to exceptional abundance of *L. pealei* are limited, with the consequence that *L. pealei* predators, such as groundfish, would have increased forage. This limitation of harvest may improve the productivity of other fishery resources of the northeast shelf ecosystem.

Finally, the investigation of environmental effects on the population dynamics and population biology of *L. pealei* remains an important research topic. Distribution and growth of *L. pealei* can be influenced by temperature (Murawski 1993; Brodziak and Macy 1996). As a result, potential global warming may substantially affect the productivity and distribution of the *L. pealei* resource. Overall, quantifying the effects of environmental variation on the growth, recruitment, maturation, and distribution of *L. pealei* will remain a challenging research topic for years to come.

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