

## Aspects of the Natural History of the Midwater Fish *Lycodapus mandibularis* (Zoarcidae) in Monterey Bay, California<sup>1</sup>

M. ERIC ANDERSON<sup>2</sup>

**ABSTRACT:** Aspects of the biology of the mesopelagic fish *Lycodapus mandibularis* are considered, primarily on the basis of closing midwater trawl samples from Monterey Bay, California. Major population centers focus in eastern North Pacific submarine canyons and deep-water inlets. The species undergoes a diel vertical migration, but not all individuals may participate in each period. Ripe individuals were found year-round and spawning is nonseasonal, probably occurring in midwater. Age estimates from otoliths showed the greatest proportion of the population sampled was of age classes III and IV, the ages at onset of maturity. The oldest individuals found were 5 years old, but estimates from the oldest fish may be biased. Feeding during the day was chiefly in surface waters, but night or day feeding in deep water may have occurred. Food items of young fish were different from those of adults but both fed heavily on planktonic crustaceans. Fish in California waters were parasitized by the nematode *Thynnascaris aduncum* and to a lesser degree by the copepod *Cardiodectes medusaeus*.

BETWEEN MARCH 1974 and January 1976, a program to study the aquarium maintenance and behavior of selected mesopelagic organisms of Monterey Bay, California, was sponsored jointly by Moss Landing Marine Laboratories, California State University and Colleges, and Steinhart Aquarium, California Academy of Sciences (McCosker and Anderson 1976). During the survey several previously rare fishes were collected regularly, including the pallid eelpout *Lycodapus mandibularis* (Zoarcidae). For the first time a large number of specimens of *L. mandibularis* were available so that the biology of the species could be investigated.

Populations of *L. mandibularis* are known from Pacific coast submarine canyons and deep-water inlets from Prince William Sound, Alaska, to off La Jolla, California (Anderson 1977; Peden and Anderson 1978). Much

taxonomic confusion has existed in the literature on *Lycodapus*, especially with *L. mandibularis*. However, Peden and Anderson (1978) clarified most of the systematic problems in the genus. Peden (1979) identified populations and investigated meristic variation in *L. mandibularis* but included little biological information on the species.

Published accounts of zoarcid biology are few as most of the literature on this family consists of systematic studies. The most important contributions to eelpout natural history (Kliever 1976; Levings 1969; Olsen and Merriman 1946; Orach-Meza 1975) were conducted on well-sampled benthic species and virtually nothing is known of the life histories of rarer, deep-living species. Though for some time members of the genus *Melanostigma* have been known to be pelagic, only 2 recent brief notes have increased knowledge of the biology of these fishes (Belman and Anderson 1979; Markle and Wenner 1979). This study is a contribution to the natural history of *L. mandibularis*, currently the most abundantly collected species in the genus. Data are presented on the distribution, reproduction, growth, food,

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<sup>2</sup>Moss Landing Marine Laboratories, Box 223, Moss Landing, California 95039. Present address: Virginia Institute of Marine Science, Gloucester Point, Virginia 23062.

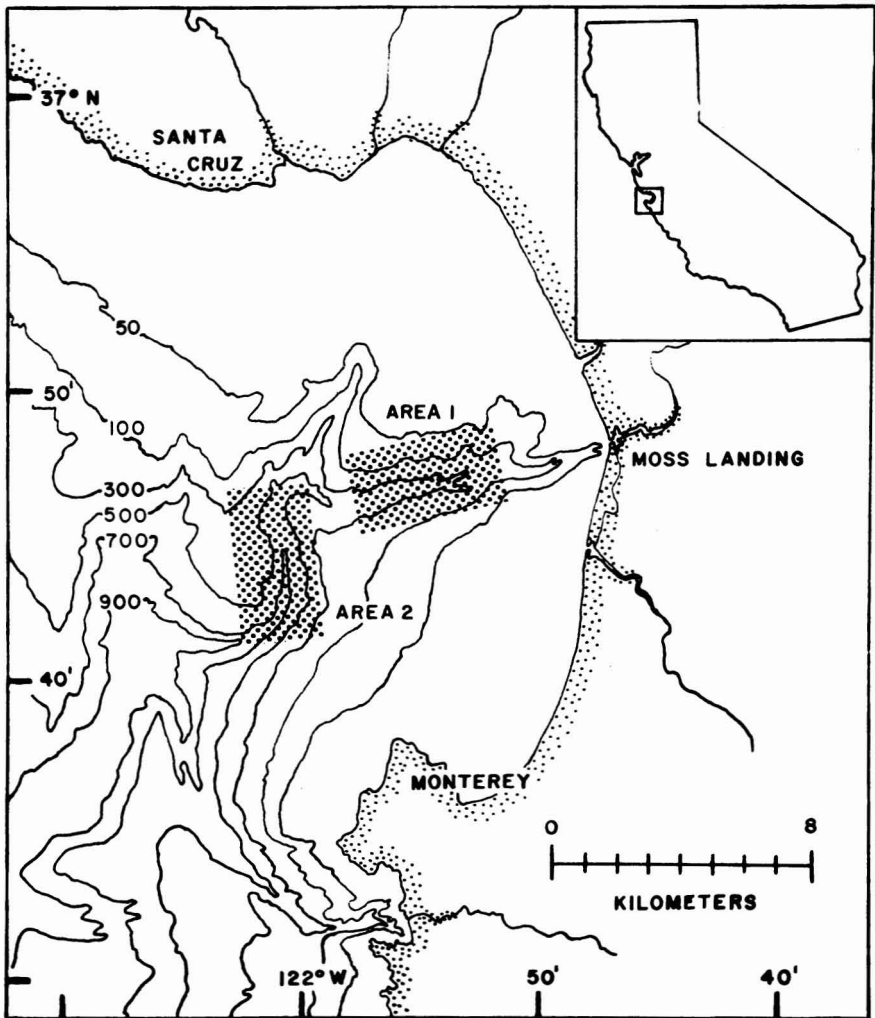


FIGURE 1. Map of Monterey Bay, California, showing the SAMMP trawling areas. Contours in fathoms.

and parasites taken from fishes collected chiefly in Monterey Bay.

#### MATERIALS AND METHODS

Most specimens considered in this study were taken during the Steinhart Aquarium Midwater Maintenance Program (SAMMP) cruises between March 1974 and January 1976 with a modified, opening-closing 1.8 m Tucker trawl (see McCosker and Anderson

1976 for details of net design). The net was towed at about 2 knots from the R/V ST-908, a converted harbor tug. The net lacked a flow meter; consequently, the volume of water filtered could not be determined precisely, but variation in time and ship speed was minimal. Two to four 1-hr hauls per cruise resulted in 56 discrete depth samples grouped in 100-m intervals from the surface to 800 m. Additional specimens were obtained from 7 quantitative tows in the upper 100 m and open net hauls. In all, 41 quantitative

samples were taken during the day and 22 at night. A total of 604 specimens of *L. mandibularis* was collected from 2 locations in Monterey Bay (Figure 1). Mean numbers of *L. mandibularis* were calculated for each 100-m interval and standardized to the total number of tows, 63. Mean volumes of planktonic crustaceans later determined to be prey of *L. mandibularis* also were calculated.

Fish used for feeding and reproductive studies were preserved on shipboard in 10 percent formalin. Preserved specimens were measured (standard length, SL) and examined for stomach contents, parasites, and reproductive condition. All gonads were excised, excess fluid and mesentery was removed, and gonads were weighed to the nearest 0.01 gm on an electronic analytical balance. Gonad indices were calculated according to the following formula (Moser 1967):

$$\text{G.I.} = \frac{\text{Wt. gonad}}{(\text{SL})^3} \times 10^{10}$$

Egg sizes were measured with an ocular micrometer to the nearest 0.1 mm. Museum specimens from other California localities were examined, but since sample size or preservation state was inadequate for detailed study, only parasites were enumerated.

Otoliths examined for age estimates were taken from 116 fresh specimens. Otoliths cleared in anise oil were readable in 1–2 hr against a black background. Marginal annuli in older fish were difficult to resolve as otoliths are thick and annuli closely spaced. Many otoliths were deemed unreadable. Consequently, age estimates of the oldest fish may be minimum estimates. Two validating criteria were used to determine if annulus formation occurred yearly: (1) otolith radius (OR), measured from focus to edge of rostrum, was plotted over time to detect any increase in marginal annulus size for the most abundantly sampled age group (age class III, i.e., fish between their second and third years); (2) temporal changes in marginal annulus translucency were studied to determine season of annulus formation. Because of small sample size and bias in selecting fish for ageing, other otolith validating criteria in use, such as agreement with Petersen's

(1895) method or back-calculation from otolith dimensions to observed fish lengths at a given age, were deemed unsatisfactory. Age-length graphs were developed for both sexes only from fish collected during winter months, due to large sample sizes during that period.

Stomach contents were identified to the lowest taxa possible. The importance of each food category was indicated by plotting the Index of Relative Importance (IRI) for juveniles and adults separately (Pinkas et al. 1971). Those fish considered juveniles were less than 110 mm SL. Also, the degree of digestion and stomach fullness were subjectively scored (after DeWitt and Cailliet 1972) to ascertain feeding chronology. Categories scored for fullness were 0, empty; 1, 1/4 full; 2, 1/2 full; 3, 3/4 full; 4, full; and for digestion state: 0, empty; 1, very digested, nothing recognizable; 2, some digestion, parts recognizable to higher taxa; 3, little digestion, much recognizable; 4, intact items, readily identifiable (Figure 2). In this technique it is assumed feeding progresses from category A through D. Chi-square tests were performed for recency of feeding; stomachs from categories B and C were considered recent and categories A and D were considered not recent. Significance of difference with depth and time in categories was determined using a two-by-two contingency table, and histograms of matrix categories were plotted against depth and time.

## RESULTS

### *Vertical Distribution*

Although nighttime samples were scarce in all depth intervals, *L. mandibularis* appeared to exhibit diel vertical migration (Figure 3). The species was present in only 3 of 15 hauls above 300 m during the day (both areas combined), whereas it occurred in 6 of 12 hauls above 300 m at night. Below 300 m capture frequencies were nearly equal; it occurred in 21 of 26 day tows (80.8 percent) and in 8 of 10 night tows. *L. mandibularis* was encountered less frequently offshore than

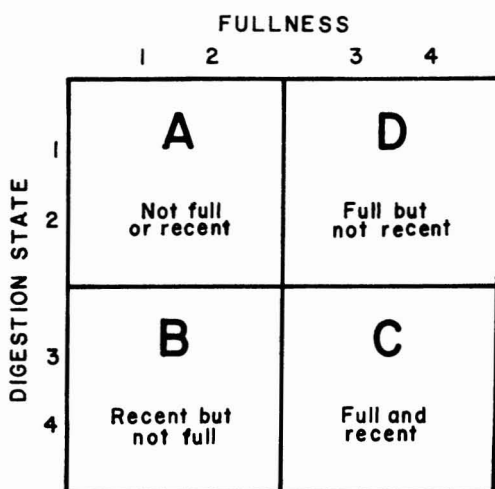


FIGURE 2. Categories of stomach contents condition (after DeWitt and Cailliet 1972).

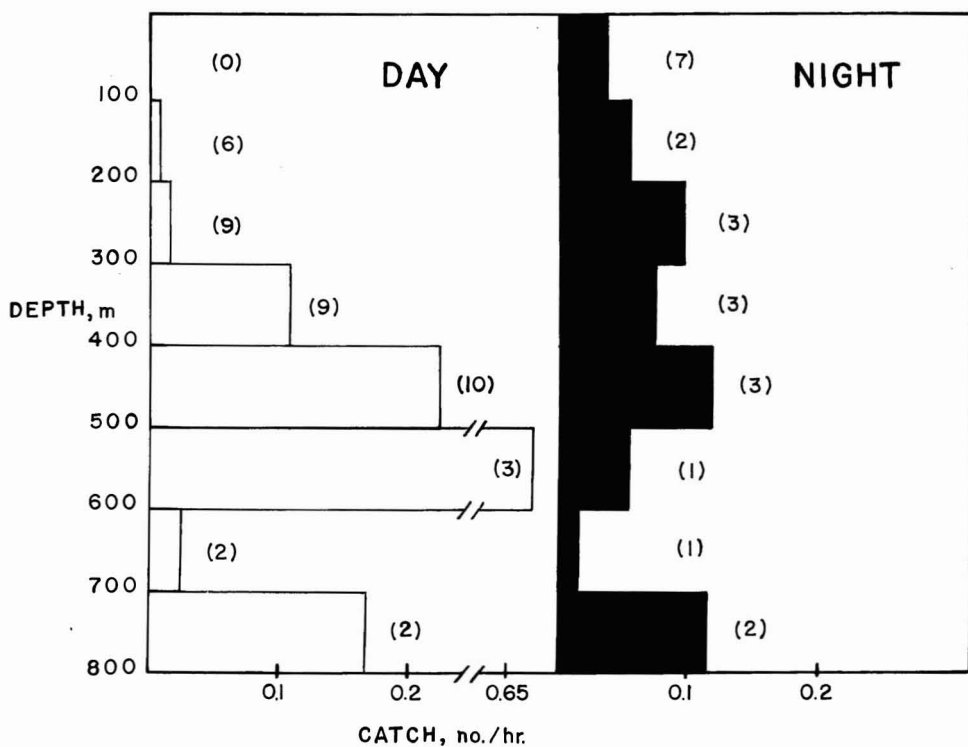


FIGURE 3. Vertical distribution of *L. mandibularis* in Monterey Canyon, localities combined. Numbers in parentheses show sample size in each depth interval.

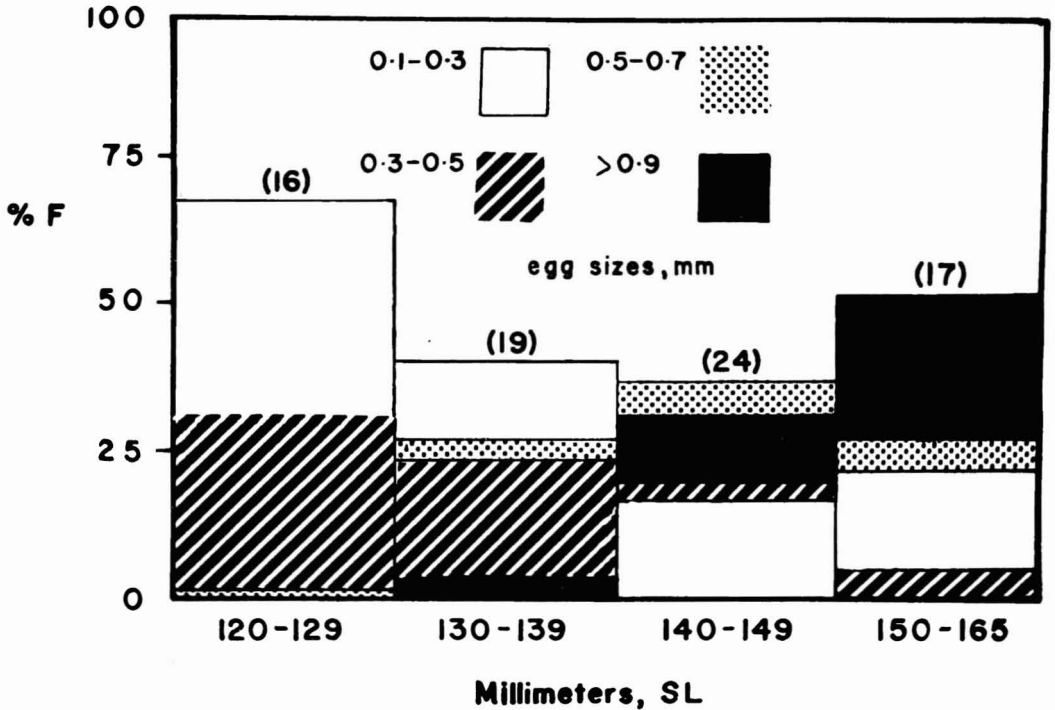


FIGURE 4. Percent frequency of egg sizes in ovaries of adult *L. mandibularis* collected between September and April. Sample sizes of each length group are in parentheses.

inshore. Offshore (area 2) the species occurred in 7 of 14 tows and inshore (area 1) in 31 of 49 tows (63.3 percent).

Postlarvae and juveniles were taken chiefly during the day below 300 m (20 of 46 hauls or 43.5 percent containing young). Above 300 m, 3 of 27 hauls (11.1 percent) contained these fish. Young fish were too scarce to allow diel differences in distribution to be detected. No differences were discernible in distribution by sex.

*Gonad Morphology and Sexual Maturity*

The testes are elongate, bilobed organs of equal size lying in the posterodorsal section of the coelom. The sperm duct lies in a dorsomedial groove along each testis and there is no specialized genital pore or papilla. Immature testes are white and rod-like with rounded anterior tips. Spawning males had greatly expanded, dark gray "leaf-like" testes

which averaged about 1/3 the liver mass. Additionally, mature males have enlarged, recurved teeth which may play a role in initiating spawning.

A single dorsomedial ovary lies in the posterior area of the body cavity in *L. mandibularis*. The oviduct is short and connects with the urinary bladder into a urogenital sinus. Immature ovaries are thin and flaccid with ova 0.05–0.2 mm in diameter, and developing eggs are readily discernible in even the smallest specimens.

Females under about 120 mm SL carried a maximum of 400 immature ova, each less than 0.2 mm in diameter. In the ripest females a complement of about 100 ± 25 eggs was observed between 1.7 and 1.9 mm in diameter (Figure 4). Eggs of this size were never seen in spent ovaries, that is, the full complement of mature eggs was evidently spawned. The number of mature complements produced annually could not be determined due to

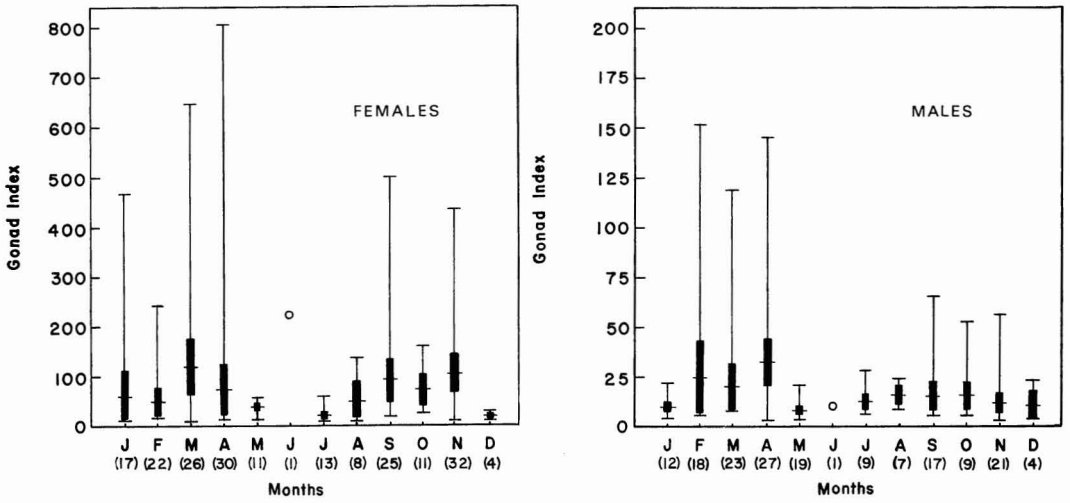


FIGURE 5. Monthly gonad indices for adult *L. mandibularis* from Monterey Bay. Vertical line and end bars represent ranges, horizontal line the mean, and dark vertical bars the 95% confidence interval. Numbers in parentheses are sample size.

inadequate samples for several months. The sex ratio of 560 fish of all ages was approximately equal with 54.3 percent females and 45.7 percent males.

*Spawning Periodicity*

Nearly equal numbers of ripe adults were taken in summer and in winter. Females considered ripe had a complement of eggs larger than 0.9 mm in diameter and gonad index values above 60. Males considered ripe exhibited inflated testes with gonad index values above 20. Chi-square tests for "ripeness" comparing summer and winter for males and females were insignificant at levels less than 0.5. In summer 43.8 percent of 80 males and 55.7 percent of 88 females were ripe. In winter 67.8 percent of 87 males and 50.9 percent of 112 females were ripe. This suggests that gonad maturation is aseasonal and that spawning may be dependent on state of individual growth and vitality.

The gonad indices for males closely paralleled those for females (Figure 5), and males reached maturity at the same age as females. Most males from winter samples had recently spawned (testes shrunken, low index values). It is difficult, however, to estimate how long

a given male has been in a spent condition, but gelatinous, expanded testes indicating recent spawning were observed in every summer month except June (both years).

*Age and Growth*

The validity of otolith annuli for ageing in *L. mandibularis* was established using two methods. First, otolith radii (OR) plotted for 49 fish of age class III generally grew larger with time (all years combined, Figure 6). Sample size was inadequate to plot OR with time for other age groups, but OR of 23 age-class-II fish measured 0.41–0.49 mm ( $\bar{x} = 0.451$ ,  $SE = 0.0049$ ). The OR of 11 fish of age classes IV and V measured 0.61–0.76 mm ( $\bar{x} = 0.692$ ,  $SE = 0.0144$ ). These data suggest the third annulus formed during one year. Second, otoliths were studied from all 116 fish to discover when hyaline "winter" and opaque "summer" margins formed. The evidence indicates an annual progression of the zones: in summer 84.8 percent of 46 fish had opaque margins, while in winter only 15.7 percent of 70 fish had opaque margins.

A maximum age of 5 years was estimated for 3 females, the largest of which measured 198 mm SL. The growth rate became nearly

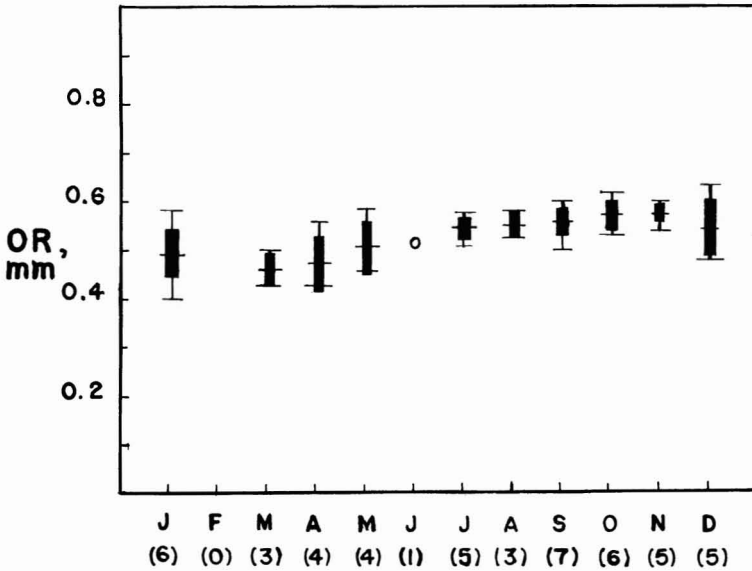


FIGURE 6. Monthly otolith radius (OR) measurements for age class III *L. mandibularis* from Monterey Bay. Graphics after Figure 5.

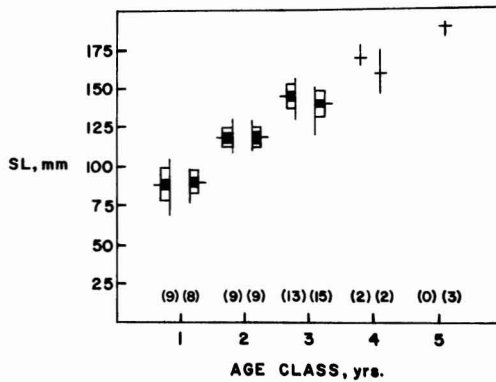


FIGURE 7. Growth relationships for *L. mandibularis* in Monterey Bay. Right, females; left, males in each age class. Sample size in parentheses. Graphics after Hubbs and Hubbs (1953).

linear after the first year and did not differ between sexes (Figure 7). The linear component of the growth relationship coupled with small sample size at the upper extreme led to a poorly fitted von Bertalanffy growth equation.

Length frequency histograms constructed for the warmer and colder periods of the year showed the greatest frequency of age

class I individuals occurring in the winter months (Figure 8). Age classes IV to VI were infrequently taken in both seasons. The greatest number of individuals taken were of age classes III and IV, the ages at onset of sexual maturity. Teeth became fully developed in males by age class III (Peden and Anderson 1978, figure 8).

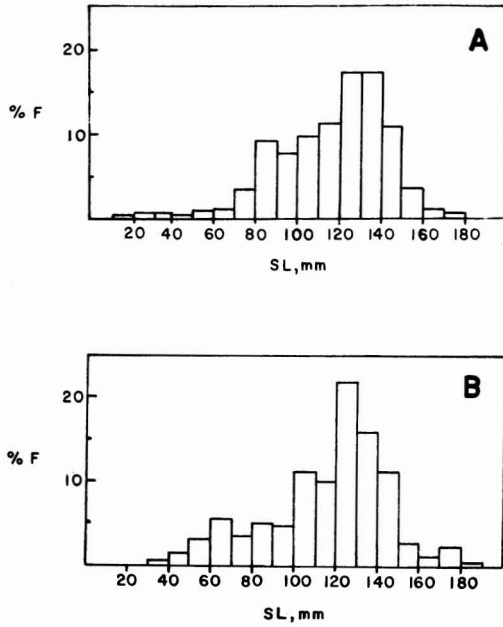


FIGURE 8. Length frequency histograms of *L. mandibularis* from Monterey Bay. A, October to March, N = 298. B, April to September, N = 261.

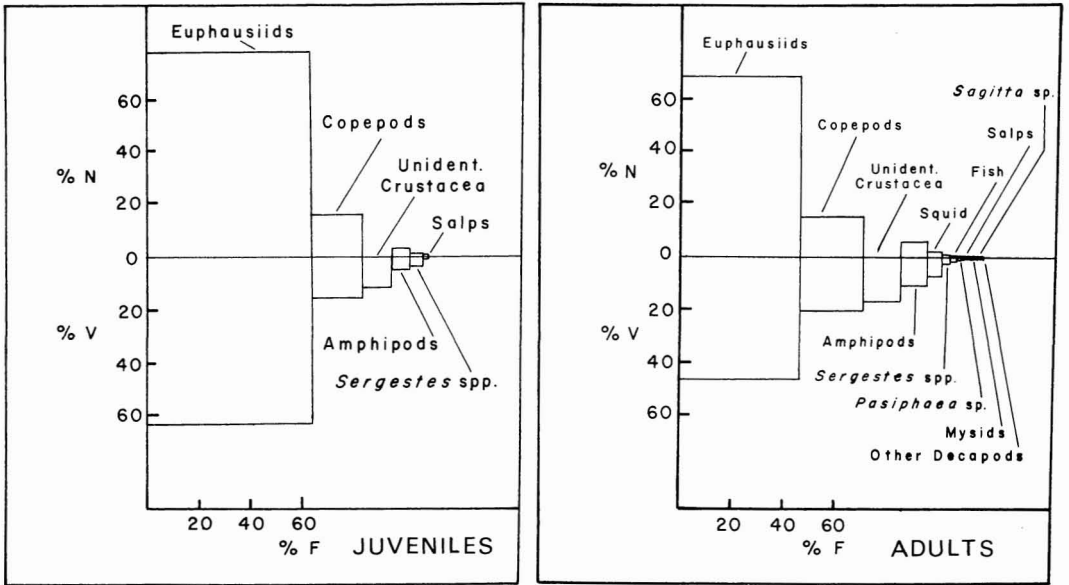


FIGURE 9. Index of Relative Importance plots for stomach items of *L. mandibularis* from Monterey Bay. % F, percentage frequency; % N, numerical percentage; % V, volumetric percentage. Sample size: adults, N = 144; juveniles, N = 111.



TABLE 1

PREY ITEMS OF 225 *L. mandibularis* TAKEN IN  
MONTEREY BAY

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Phylum: Arthropoda
Order: Copepoda
<i>Calanus</i> sp.
unidentified calanoids
<i>Pareuchaeta japonica</i>
Order: Euphausiacea
<i>Euphausia pacifica</i>
<i>Thysanoessa spinifera</i>
unidentified euphausiids
Order: Amphipoda
<i>Orchomene obtusa</i>
<i>Paracallisoma coecus</i>
unidentified gammarideans
<i>Hyperia medusarum</i>
<i>Stilipes distincta</i>
<i>Paraphronima</i> sp.
<i>Primno macropa</i>
unidentified hyperiids
Order: Mysidacea
<i>Boreomysis japonica</i>
Order: Decapoda
<i>Sergestes similis</i>
<i>Sergestes halia</i> (?)
<i>Pasiphaea pacifica</i>
<i>Pasiphaea</i> sp.
Order: Decapoda
<i>Gennadas propinquus</i>
<i>Pandalus jordani</i>
unidentified decapods
Phylum: Mollusca
Order: Teuthoidea
<i>Gonatus onyx</i>
<i>Gonatus</i> sp.
<i>Octopoteuthis deletron</i>
unidentified squid
Phylum: Chaetognatha
<i>Sagitta</i> sp.
Phylum: Chordata
Salpidae, unidentified
<i>Stenobranchius leucopsarus</i>
<i>Cyclothone signata</i>
<i>Leuroglossus stilbius</i>

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### Food Habits

PREY ITEMS: *Lycodapus mandibularis* ate a wide variety of prey items (Table 1). Juveniles ate chiefly euphausiids and copepods in similar proportions to adults, but other food, such as squid and large shrimp, was found only in stomachs of adult fish (Figure 9).

A diel periodicity has been shown for the

vertical distribution of several prey species of *L. mandibularis* (Anderson 1978; Brinton 1976; Frost and McCrone 1979; Pearcy 1972, 1977; Pearcy et al. 1977; Roper and Young 1975; Youngbluth 1976). In this study, although net mesh size precluded an analysis of the distribution of smaller prey, larger prey were found in greater numbers above 300 m at night, with some groups concentrating in the upper 100 m (Anderson 1977).

FEEDING CHRONOLOGY: The frequency of the four categories of fullness and digestion state (Figure 2) for 225 stomachs with food showed only a slightly greater number with well-digested food at night. A chi-square test among categories to test day-night differences in feeding was insignificant.

Correlating the two recent (B and C) and two not recent (A and D) categories with depth during day and night showed that during the day fish that had fed most recently were captured above 400 m (Figure 10). Combining the 0–200 m and 200–400 m intervals of Figure 10 and testing for recency in day-caught fish gave a  $\chi^2$  value of 5.024, significant at  $p < 0.025$ , 1 df. Similarly, combining the two deeper intervals (400–600 m and 600–800 m) showed most night-caught fish had recently fed ( $\chi^2 = 18.917$ , significant at  $p < 0.001$ , 1 df).

These results suggest daytime feeding occurs in shallow depth intervals; most recently fed fish were found there as were most empty stomachs (62.6 percent of shallow-caught fish versus 41.8 percent of deep-caught fish). At night, most recently fed fish were caught deep, but 57.1 percent of the sample there had empty stomachs while 50.0 percent of shallow-caught fish had empty stomachs.

### Parasites

The point of attachment and frequency of parasites were noted on examination of the internal organs of 575 *L. mandibularis* from all California localities. The most abundant parasite encountered was the nematode *Thynnascaris aduncum* (larvae); 29.2 percent of the adults and 15.2 percent of the juveniles carried one or more of these worms. The

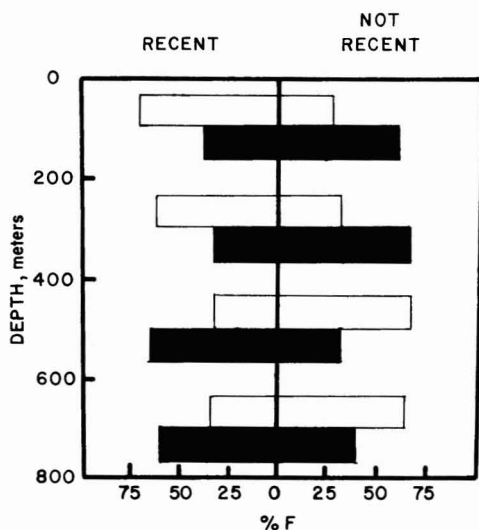


FIGURE 10. Day-night histograms from feeding chronology matrices of stomach contents in *L. mandibularis* from Monterey Bay. Light bars, day samples; dark bars, night samples. Sample size: day, recent, N = 86, not recent, N = 129; night, recent, N = 17, not recent, N = 21.

nematode was found attached to the stomach and intestinal walls, peritoneum, gonad, liver, heart, and beneath the skin over the epaxial muscles. The greatest number of worms found in one fish was 8 in a very emaciated female, but most parasitized fish contained fewer than 3 nematodes. The copepod *Cardiodectes medusaeus* was observed in only 15 fish. It was found attached to the gill arch or isthmus area of *L. mandibularis* and is well known from other mesopelagic fishes (Noble and Collard 1970).

#### DISCUSSION

The majority of *L. mandibularis* captures have come from the vicinity of submarine canyons and deep inlets (Peden 1979; Peden and Anderson 1978). Two collections from California outside canyons (nonquantitative bottom trawls off Cape San Martin and Point Arguello) indicate the species probably occurs along the open slope. Although obtaining only 2 collections of the species from several dozen deep hauls along the California slope that I have studied indicates the species may be rare there, this conclusion is misleading. Its small size and pelagic habitat warrant

its scarcity in bottom trawls. Collections of *L. mandibularis* in northern waters considerably away from canyons and inlets are presently unknown.

Peden (1979) suggested there may be little movement of fish between western Canadian inlets if they avoid out-flowing, near-surface waters. As yet, diel vertical migration in northern populations has not been satisfactorily demonstrated and orientation to specific water masses or currents is unknown in *L. mandibularis*. An analysis of the hydrography of Monterey Bay may clarify some of the factors governing the distribution of *L. mandibularis* and other mesopelagic species inhabiting submarine canyons and deep inlets.

Seasonal hydrographic changes have a marked influence on the temporal distribution of several mesopelagic species in Monterey Bay (Aughtry 1953; Barham 1957; Fast 1960). Fast provided a review of the hydrography of the bay as it affected the distribution of the lanternfish *Stenobrachius leucopsarus*. He reported that during the "Oceanic" period (generally July to October), offshore water moved into the bay bringing an "invasion" of plankton that concentrated in the canyon. During the winter (the

“Davidson Current” period) the greatest increase in the population of *Stenobranchius* in the bay occurred. Later, from February to July (“Upwelling” period), a decrease in the population of older *Stenobranchius* occurred. Fast (1960) concluded that as the fish moved into surface waters at night they were swept offshore by this subsurface movement.

Although no seasonality of the local *L. mandibularis* population was detected throughout this study, during periods of strong summer upwelling in which surface water is moved offshore, individuals that concentrate in shallow water could, conceivably, be moved out of the bay as Fast (1960) predicted for *Stenobranchius*. During the subsequent “Oceanic” season (July to October), they then may be returned to in-shore areas as Percy (1976) showed for micronekton off Oregon. Seasonal hydrographic changes have a marked effect on the abundance of the planktonic food of *L. mandibularis* (Colebrook 1977; Hebard 1966; Laurs 1967; Youngbluth 1976) and an advantage would be given to those populations of *L. mandibularis* with a more stable food supply, that is, those able to resist dispersion into food-poor oceanic waters. But do canyons have a more stable food supply for these fishes, especially during summer upwelling periods when plankton is moved offshore? Unfortunately, there are no quantitative data available to compare plankton abundances between canyons and adjacent areas in order to evaluate this question.

Diel vertical migration in mesopelagic species in order to feed in richer surface waters is well documented (Baird et al. 1975; Brinton 1976; Clarke 1974, 1978; DeWitt and Cailliet 1972; Gorelova 1974, 1975; Isaacs et al. 1974; Percy 1970; Percy et al. 1979; Pearre 1973; Youngbluth 1976). For abundant groups like euphausiids (Youngbluth 1976) or myctophids (Percy et al. 1979), population movements can be blurred by some individuals remaining at depth on a given night while others migrate. The feeding chronology and vertical distribution of *L. mandibularis* suggest that fish may migrate into surface waters at night or early dawn to feed. The data also support the hypothesis that fish caught at night in deep water may have fed there or

in intermediate depths and not in shallow water the day before capture. However, night-caught fish in deep water of low temperature may experience reduced metabolic activity and slowed digestion rates (Percy et al. 1979). This would mask the time and place of feeding both of fish that remained deep and of those that migrated upward.

There is some information on the spawning of oviparous eelpouts, but much of it is brief because of inadequate observations. Mead et al. (1964) suggested zoarcids aggregate and produce demersal eggs that develop close to the bottom. Parental care and nesting, or burrowing, has been implied for the benthic species *Macrozoarces americanus* (Olsen and Merriman 1946; Orach-Meza 1975; White 1939), *Lycodopsis pacifica* (Levings 1969), and *Maynea californica* (Kliever 1976).

No evidence exists that *L. mandibularis* utilizes the sea bottom for spawning, and a pelagic spawning without parental care seems most parsimonious for this species. Markle and Wenner (1979) supplied some convincing evidence that the mesopelagic eelpout *Melanostigma atlanticum* shoals near the bottom to spawn in the North Atlantic. Their evidence consisted of a seasonal (summer) increase in captures by bottom trawls which correlated with maximum ova diameters and a shift to a typically benthic parasite fauna. In *L. mandibularis*, a species with a similar habitat and ecology, spawning, hence maximum ova diameters, was aseasonal and the parasite fauna was more typical of mesopelagic fishes. This suggests *L. mandibularis* may not shoal near the bottom for spawning, but no direct observations have been made. A wide range in the vertical distribution of postlarvae was observed for both day and night collections; hence, metamorphosis may not be restricted to the lighted surface waters in *L. mandibularis* as it is for other mesopelagic species (Marshall 1954).

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#### LITERATURE CITED

- ANDERSON, M. E. 1977. Systematics and natural history of the midwater fish *Lycodapus mandibularis* Gilbert in California waters. M.A. Thesis. California State University, Hayward.
- . 1978. Notes on the cephalopods of Monterey Bay, California, with new records for the area. *The Veliger* 21(2):255–262.
- AUGHTRY, R. H. 1953. The biology and ecology of *Cyclothone signata* Garman in the Monterey Bay area. M.A. Thesis. Stanford University, Stanford, Calif.
- BAIRD, R. C., T. L. HOPKINS, and D. F. WILSON. 1975. Diet and feeding chronology of *Diaphus taaningi* (Myctophidae) in the Cariaco Trench. *Copeia* 1975:356–365.
- BARHAM, E. G. 1957. The ecology of sonic scattering layers in the Monterey Bay area, California. Ph.D. Thesis. Stanford University, Stanford, Calif.
- BELMAN, B. W., and M. E. ANDERSON. 1979. Aquarium observations on feeding by *Melanostigma pammelas* (Pisces, Zoarcidae). *Copeia* 1979:366–369.
- BRINTON, E. 1976. Vertical migration and avoidance capability of euphausiids in the California Current. *Limn. Ocean.* 12:451–483.
- CLARKE, T. A. 1974. Some aspects of the ecology of stomiatoid fishes in the Pacific Ocean near Hawaii. *Fish. Bull.* 72(2):337–351.
- . 1978. Diel feeding patterns of 16 species of mesopelagic fishes from Hawaiian waters. *Fish. Bull.* 76(3):495–513.
- COLEBROOK, J. M. 1977. Annual fluctuations in biomass of taxonomic groups of zooplankton in the California Current, 1955–59. *Fish. Bull.* 75(2):357–368.
- DEWITT, F. A., JR., and G. M. CAILLIET. 1972. Feeding habits of two bristlemouth fishes, *Cyclothone acclinidens* and *C. signata* (Gonostomatidae). *Copeia* 1972:868–871.
- FAST, T. N. 1960. Some aspects of the natural history of *Stenobrachius leucopsarus* Eigenmann and Eigenmann. Ph.D. Thesis. Stanford University, Stanford, Calif.
- FROST, B. W., and L. E. MCCRONE. 1979. Vertical distribution, diel vertical migration, and abundance of some mesopelagic fishes in the eastern subarctic Pacific Ocean in summer. *Fish. Bull.* 76(4):751–770.
- GORELOVA, T. A. 1974. Zooplankton from the stomachs of juvenile lanternfish of the family Myctophidae. *Oceanol., Acad. Sci., USSR* 14(4):575–580.
- . 1975. The feeding of fishes of the family Myctophidae. *J. Ichthyol.* 15(2):208–219.
- HEBARD, J. F. 1966. Distribution of Euphausiacea and Copepoda off Oregon in relation to oceanographic conditions. Ph.D. Thesis. Oregon State University, Corvallis.
- HUBBS, C. L., and C. HUBBS. 1953. An improved graphical analysis and comparison

- of series of samples. *Syst. Zool.* 2(2):49–56.
- ISAACS, J. D., S. A. TONT, and G. L. WICK. 1974. Deep-scattering layers: vertical migration as a tactic for finding food. *Deep-Sea Res.* 21(8):651–656.
- KLIEVER, R. G. 1976. Natural history of *Maynea californica* (Pisces: Zoarcidae) in a drift seaweed habitat in the Monterey Submarine Canyon, Monterey Bay, California. M.A. Thesis. California State University, San Jose.
- LAURS, R. M. 1967. Coastal upwelling and the ecology of lower trophic levels. Ph.D. Thesis. Oregon State University, Corvallis.
- LEVINGS, C. D. 1969. The zoarcid *Lycodopsis pacifica* in outer Burrard Inlet, British Columbia. *J. Fish. Res. Bd. Can.* 26:2403–2412.
- MARKLE, D. F., and C. A. WENNER. 1979. Evidence of demersal spawning in the mesopelagic zoarcid fish *Melanostigma atlanticum* with comments on demersal spawning in the alepocephalid fish *Xenodermichthys copei*. *Copeia* 1979:363–366.
- MARSHALL, N. B. 1954. Aspects of deep sea biology. Hutchinson, London. 380 pp.
- MCCOSKER, J. E., and M. E. ANDERSON. 1976. Aquarium maintenance of mesopelagic animals: a progress report. *Bull. So. Calif. Acad. Sci.* 75(2):211–219.
- MEAD, G. W., E. BERTELSEN, and D. M. COHEN. 1964. Reproduction among deep-sea fishes. *Deep-Sea Res.* 11:569–596.
- MOSER, H. G. 1967. Reproduction and development of *Sebastes paucispinis* and comparison with other rockfishes off southern California. *Copeia* 1967:773–797.
- NOBLE, E. R., and S. B. COLLARD. 1970. The parasites of midwater fishes. Pages 57–68 in S. F. Snieszko, ed. A symposium on diseases of fishes and shellfishes. *Am. Fish. Soc. Spec. Publ.* 5, Washington, D.C.
- OLSEN, Y., and D. MERRIMAN. 1946. Studies on the marine resources of southern New England. IV. The biology and economic importance of the ocean pout, *Macrozoarces americanus* (Bloch and Schneider). *Bull. Bingham Ocean. Coll.* 9(4):1–184.
- ORACH-MEZA, F. L. 1975. Distribution and abundance of ocean pout, *Macrozoarces americanus* (Bloch and Schneider) 1801 in the western North Atlantic Ocean. M.S. Thesis. University of Rhode Island, Kingston.
- PEARCY, W. G. 1970. Vertical migration of the ocean shrimp *Pandalus jordani*: a feeding and dispersal mechanism. *Calif. Fish Game* 56(2):125–129.
- . 1972. Distribution and ecology of oceanic animals off Oregon. Pages 351–377 in A. T. Pruter and D. L. Alverson, eds. *The Columbia River estuary and adjacent ocean waters*. Univ. Washington Press, Seattle.
- . 1976. Seasonal and inshore-offshore variation in the standing stocks of micronekton and macrozooplankton off Oregon. *Fish. Bull.* 74(1):70–80.
- . 1977. Variations in abundance of sound scattering animals off Oregon. Pages 647–666 in R. N. Philbrick, ed. *Ocean sound scattering prediction*. Plenum Press, New York.
- PEARCY, W. G., E. E. KRYGIER, R. MESECAR, and F. RAMSEY. 1977. Vertical distribution and migration of oceanic micronekton off Oregon. *Deep-Sea Res.* 24:223–245.
- PEARCY, W. G., H. V. LORZ, and W. PETERSON. 1979. Comparison of the feeding habits of migratory and non-migratory *Stenobranchius leucopsarus* (Myctophidae). *Mar. Biol.* 51:1–8.
- PEARRE, S. 1973. Vertical migration and feeding in *Sagitta elegans* Verrill. *Ecology* 54(2):300–314.
- PEDEN, A. E. 1979. Meristic variation of *Lycodapus mandibularis* and oceanic upwelling on the west coast of North America. *J. Fish. Res. Bd. Can.* 36(1):69–76.
- PEDEN, A. E., and M. E. ANDERSON. 1978. A systematic review of the fish genus *Lycodapus* (Zoarcidae) with descriptions of two new species. *Can. J. Zool.* 56:1925–1961.
- PETERSEN, C. G. J. 1895. Eine Methode zur Bestimmung des Alters und Wuchses der Fische. *Mitth. Deutsch Seefisch.-Ver.* 11:226–235.
- PINKAS, L., M. OLIPHANT, and I. L. K. IVERSON. 1971. Food habits of albacore, bluefin tuna and bonito in California

- waters. Calif. Fish Game Bull. 152:1-105.
- ROPER, C. F. E., and R. E. YOUNG. 1975. Vertical distribution of pelagic cephalopods. Smithsonian Contr. Zool. (209):1-51.
- WHITE, H. C. 1939. The nesting and embryo of *Zoarces anguillaris*. J. Fish. Res. Bd. Can. 4(5):337-338.
- YOUNGBLUTH, M. J. 1976. Vertical distribution and diel migration of euphausiids in the central region of the California Current. Fish. Bull. 74(4):925-936.