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Title: Reproduction, Growth, Feeding, and Distribution of the Mesopelagic Fish Tactostoma macropus

Redacted for Privacy

Abstract approved: ______________________

Professor William G. Pearcy

Over 5,000 specimens of *Tactostoma macropus* Bolin, 1939 were collected off Oregon between 1961 and 1978 with Isaacs Kidd midwater trawls (IKMT) and a large pelagic trawl. *T. macropus* spawned off Oregon mainly during the summer months. Oocytes matured in batches with probably only one batch maturing each year. Number of ripening oocytes ranged from 24,553 to over 66,000 in the ovaries examined. Females matured at lengths of 300 mm or more. Metamorphosis occurred during the fall and winter and small juvenile fish (50-70 mm) were consistently recruited into the IKMT catches in the winter.

Differences between the length-frequency distributions of fish in catches made with the IKMT and those made with a larger pelagic trawl suggest that larger *T. macropus* usually avoid the IKMT. The occurrence of large fish (greater than 300 mm S. L.) in both day and night catches at depth and their virtual absence in catches in near

surface waters suggest that unlike smaller *T. macropus* larger fish undertake limited or no diel vertical migrations.

Growth curves derived from length-frequency analysis, otolith aging and back calculation from otoliths were similar. Average length at age one year was around 110 mm, at age two years 165 mm, and at age three years 200 mm. Extrapolation of growth curves gave a predicted average age at first spawning in females of at least six years.

Small *T. macropus* (51-150 mm) fed chiefly on euphausiids, primarily *Euphausia pacifica*. With increases in length (151-250 mm+) euphausiids became less important while decapods (primarily *Sergestes similis*) and fish (primarily myctophids) became more important in the diet. There was little evidence for either diel peridicity in feeding or seasonal changes in diet.

T. macropus appears to be most abundant in the eastern Subarctic and Transitional Regions of the North Pacific Ocean. Between approximately 45°N and 50°N latitude it is abundant over a large longitudinal range.

Reproduction, Growth, Feeding, and Distribution of the Mesopelagic Fish *Tactostoma macropus*

by

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REPRODUCTION, GROWTH, FEEDING, AND DISTRIBUTION OF THE MESOPELAGIC FISH *Tactostoma macropus*

INTRODUCTION

Tactostoma macropus Bolin, 1939, a mesopelagic fish in the family Melanostomiatidae (see Morrow and Gibbs, 1964 for a discussion of the family) is the only common melanostomiatid fish collected off Oregon. It was generally among the four most abundant mesopelagic fish in the upper 200 meters at night in the region just past the continental slope off the central Oregon coast and therefore is an important species in the mesopelagic community (Pearcy, 1964; Pearcy and Laurs, 1966; Pearcy et al., 1977).

As many other mesopelagic fishes do, smaller *T. macropus* undertake diel vertical migrations. The center of its daytime distribution off Oregon is between 400 and 600 meters whereas at night it is most abundant in the upper 200 meters (Pearcy et al., 1977).

Little is known of the biology of stomiatoid fishes, however, and *T. macropus* is no exception. The only previous study that examined aspects of its biology was that of Robison (unpublished thesis, 1973). His study was based on only 221 specimens collected in the California Current. The present study, based on over 5,000 specimens collected mainly off Oregon between 1961 and 1978 describes the reproduction, growth, feeding, and geographical distribution of this common mesopelagic fish.

METHODS

General

This study is based mainly on the collection of *T. macropus* from a series of over 2400 pelagic hauls conducted by Oregon State University off Oregon between 1961 and 1978. Much of the sampling was concentrated in the vicinity of 44°40'N, 125°35'W over the outer continental slope, although other regions off Oregon were also sampled.

Most hauls were with a 2.4 m^2 or 5.4 m^2 (mouth area) Isaacs Kidd Midwater Trawl (IKMT) lined with 5 mm (bar measure) mesh. After 1962 the trawl was fitted with an eight or five net Multiple Plankton Sampler (MPS), the cod ends of which were of 0.57 mm plankton netting. Additional data came from several hauls with a large (approximately 65 m^2 mouth area) pelagic trawl lined with 19 mm (stretch measure) mesh, and from a series of oblique bongo net hauls (200 m to the surface) off Oregon.

Sampling was generally in the upper 1000 m. Nets in the MPS could be opened and closed on command from the surface or set to open at predetermined intervals. Depth was monitored and discrete depth intervals were sampled. (See Pearcy, 1964 and Pearcy et al., 1977 for discussions of the sampling procedures.)

Tactostoma macropus was collected in over 800 hauls between

1961 and 1978. Fish were preserved on board ship in 10% formaldehyde solution and were later transferred to 20% and then 45% isopropyl alcohol in the laboratory. Standard lengths of preserved specimens were determined to the nearest millimeter.

In addition to the O. S. U. specimens five fish on loan from the University of Washington, two specimens from the Provincial Museum of British Columbia and two specimens from the University of Tokyo were examined.

Reproduction

The size ranges of oocytes in ovaries from 490 fish were recorded and size-frequency distributions of oocytes in the ovaries of fourteen large (293 mm - 382 mm S. L.) females were determined. All measurements were of preserved material. A cross section of one lobe of each ovary was removed and examined under 30 power with a stereomicroscope fitted with an ocular micrometer. Oocytes were teased out of the ovarian tissue and all oocytes greater than 0. 13 mm in diameter were counted. In two specimens sections from the anterior, mid, and posterior ovary were examined. The size-frequency distributions of oocytes in each section were very similar indicating that the distribution in a cross-section is independent of the section's position in the ovary.

Based on the size-frequency distributions and appearance of the oocytes, six stages of ovarian maturity were defined:

Stage I. Largest oocytes were less than 0.10 mm in diameter; oocytes were transparent.

Stage II. Largest oocytes were 0.10 mm to 0.20 mm in diameter; cytoplasm was granular in appearance; larger oocytes were semi-opaque.

Stage III. Largest oocytes were 0.20 mm to 0.30 mm in diameter <u>or</u> a mode of opaque oocytes was centered between 0.20 mm and 0.30 mm diameter.

Stage IV. A mode of opaque oocytes was centered between 0.30 mm and 0.60 mm diameter.

Stage V. A mode of opaque or translucent oocytes was centered at 0.60 mm or greater diameter; oocytes were bound up in the connective tissue of the ovary.

Stage VI. Oocytes were translucent and loose in the ovarian lumen.

Fish collected in different months were examined for stage of ovarian maturity and the percentage of fish in each of four length groups at each stage of maturity was determined for each month. Gonadal indices (gonadal wet wt./total fish wet wt. X 100) were determined for large males (270 + mm S. L.) to determine if a seasonal cycle in the index was present. Length-frequency distributions of monthly catches of fish were examined to determine if there was a seasonal pattern of recruitment of small *T. macropus* into the catches.

Fecundity in eight ripe or nearly ripe females was estimated by measuring the volume of each ovary and a small cross-section of each ovary; determining the number of ripe or ripening oocytes in each section; and then solving the equation:

$$\frac{\text{no. ripening oocytes in the section}}{\text{volume of section}} \times \text{volume of entire ovary} = \text{fecundity.}$$

Growth

Length-frequency distributions of monthly catches of *T. macropus* from off Oregon were plotted sequentially (1961-1976) and examined for modal progressions that might reflect growth. Otoliths were removed from 166 fresh or frozen fish; 154 of these fish were collected in May and July 1976 and the other 12 fish were collected in September 1974 and 1975. The otoliths were taped to cardboard sheets for storage. Otoliths were examined under reflected light in water or glycerine with a stereomicroscope. Photographs were taken of most of those otoliths having a readible structure. The greatest diameter of each otolith was measured either directly through a stereomicroscope fitted with an ocular micrometer or from photographs using a conversion factor (1.0 mm on print = 0.0230 mm actual measure). Diameters of each of the hyaline rings were determined. Measurements were to the center of each ring.

Feeding Habits

Stomach contents from 530 fish and intestinal contents from 483 fish collected off Oregon between 1971 and 1977 were examined.

Four stages of fullness were recognized:

Stage 0. Stomach empty and thick walled.

Stage 1. Stomach partially full.

Stage 2. Stomach full and slightly distended.

Stage 3. Stomach very full, greatly distended and thin walled.

Stage of fullness was recorded for each stomach. Three stages of digestion were recognized:

Stage 1. Food well preserved; little dismemberment; flesh may be firm.

Stage 2. Food partially digested; flesh soft; some dismemberment.

Stage 3. Food well digested; flesh soft or completely disintegrated; much dismemberment; in crustaceans only exoskeleton may remain, in fish only the bones or chunks of flesh.

When food at more than one stage of digestion was present in a stomach all stages of digestion for that stomach were recorded. Taxa were identified as specifically as possible. Most food items were measured. Carapace lengths of euphausiids and shrimps and standard lengths (S. L.) of fishes were measured. Carapace lengths of Euphausia pacifica were converted to total lengths using the formula in Smiles and Pearcy (1971). The number and taxa of food items in each stomach were recorded. Stomachs from T. macropus collected at different times of the year, at different times of the day and at different depths were examined in an attempt to determine whether there were seasonal or diel changes in feeding.

Distribution

The literature was examined for locations of catches of *T. macropus*. Data presented in Aron (1960) was analyzed in detail.

RESULTS AND DISCUSSION

Reproduction

Morphology of the Ovary

The ovary of _T. macropus_ is a long, bilobate structure stretching the entire length of the abdominal cavity. Oocytes in each lobe are imbedded in a series of parallel folds oriented at an angle slightly less than 90° to the long axis of the lobe.

Ovarian Development

Size-frequency distributions of oocytes from five ovaries show the progressive increase in size of maturing oocytes (Figs. 1A-1E). Ripe ovaries from six fish collected in early September 1978 off Oregon were examined. In one ripe ovary mature oocytes ranged from approximately 0.81 mm to 1.26 mm in diameter, with 65% between 1.00 mm and 1.13 mm in diameter (Fig. 1E). The size ranges of mature oocytes in the other five ripe ovaries were similar. Mature oocytes were transluscent with segmented yolk and a single oil globule ranging in size from 0.23 mm to 0.32 mm in diameter. The presence of several to many smaller oil bodies in nearly mature oocytes suggests that the single large oil globule coalesces from these smaller bodies. A clear perivitelline space up to 0.20 mm wide was

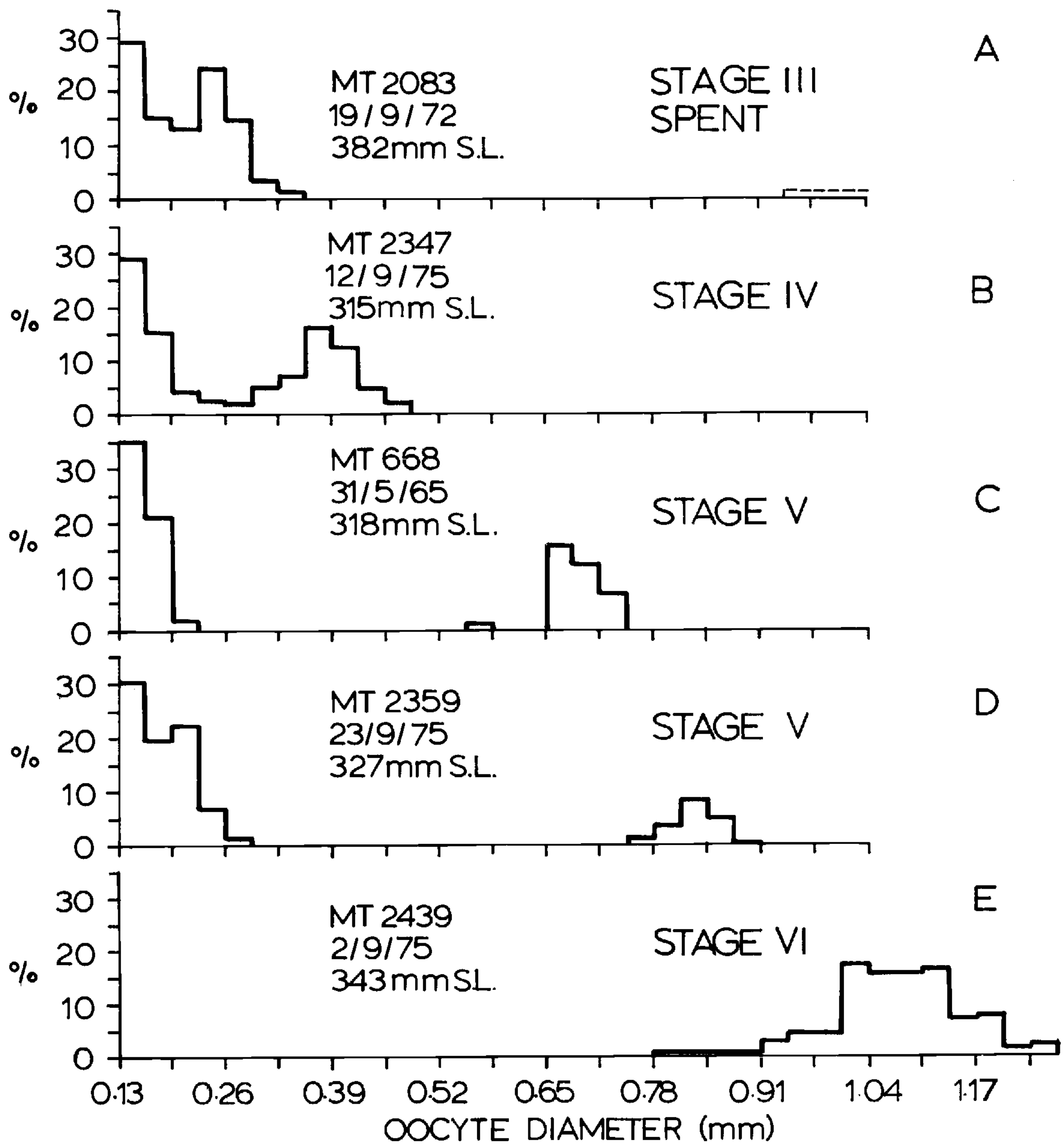


Figure 1. Oocyte size-frequency distributions and corresponding stages of maturity for five fish. In the ripe ovary the small oocytes were not counted, but the largest of these smaller oocytes were around 0.32 mm with many around 0.26 mm in diameter.

present in many of the mature oocytes.

Ten spent ovaries from fish collected in September off Oregon were examined. In the lumen of each were found several (up to 23) large, unexpelled oocytes. These large oocytes were very similar in appearance and size to those mature oocytes found in ripe ovaries and the large oil globule was distinct in most. The ovaries were quite flaccid and spawning had probably occurred recently in these fish.

Based on the size-frequency distributions of the mass of smaller oocytes in these spent ovaries, seven were at maturity stage II and three were at maturity stage III. One stage III ovary from a fish collected in November 1962 contained four large (0.65 mm - 0.81 mm), wrinkled objects that were probably old unexpelled oocytes from a previous spawning.

Oocytes are spawned in batches (Fig. 1). Although there is a possibility that the small opaque oocytes present in ripe ovaries may mature during the same year as those in the advanced mode, data to be presented suggest that spawning in _T. macropus_ is seasonal, so that more than one spawning per year is unlikely.

Fecundity and Gonadal Index

Estimates of fecundity and gonadal index in seven Stage V females and in one ripe female appear in Table 1. The number of

TABLE 1. Fecundity and Gonadal Index of Eight Stage V and VI Female *T. macropus*.

Standard length (mm)	360[+]	347	311	316	312	318	311	327
Total wet weight (g)	130	98.4	64.3	61.1	69.6	56.5	53.5	53.5
Ovary wet weight (g)	42 ml*	18.4	15.7	12.5	11.9	7.6	5.8	9.0
Gonadal Index	32	18.7	24.4	20.5	17.1	13.5	10.9	16.8
Fecundity	66,000	64,860	54,361	52,513	42,112	35,778	33,988	24,553

+ Fish collected off Japan

* Many loose oocytes so ovary was not weighed but the displacement was measured

ripening or ripe oocytes in each ovary ranged from approximately 24,000 to 66,000. Gonadal indices ranged from 10.9 to 24.4 in the Stage V fish and the index was about 32 in the ripe female.

Tactostoma macropus is similar to many other pelagic spawners in having very high fecundity and gonadal index. This suggests that egg and larval mortality is very high and that much energy is devoted to reproduction. Higham and Nicholson (1964) found a similar range (10-34) in gonadal index for ripe Brevoortia tyrannus (Atlantic menhaden), another pelagic spawner.

Size at Maturity

In Table 2 the numbers of fish containing ovaries at each stage of maturity are shown for each of four length groups of fish and for different months of the year. In the first two length groups (151 mm-250 mm) all ovaries were at Stage I or II. In the 251 mm - 300 mm length group ovaries at Stages I, II, and III were found. Ovaries at Stages IV, V, or VI and spent ovaries were found only in fish 305 mm or longer suggesting that first spawning in female T. macropus occurs at around this length.

Season of Reproduction

Of the 50 ovaries from large female T. macropus (301 mm+) collected off Oregon or Washington from May through September and

TABLE 2. Ovarian Maturity Stages of Different Sized *T. macropus* Collected in Different Months. Numbers of Fish at Each Maturity Stage are in Parentheses. All Fish Examined for Stage of Maturity are Included in the Table.

Fish Length (mm)	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
151-200	I(2)	I(4)		I(7)	I(6)	I(5)	I(4) I or II(146)*		I(54)		I(9)	
201-250	I(1)	I(3)		I(3)	I(4)	I(1)	I(4) I or II(94)*		I(20) II(1)		I(8)	
251-300	I(1)	II(2)	I(1)	I(1)		I(4) II(1)	I(7) II(7) I or II(8)* III(3)	I(2) II(2)	I(7) II(11) III(2)		III(1)	I(1) II(1)
301+					III(1) V(1)	IV(1) V(2)	II(1) V(2) VI(1)+	III(2) V(1)	II(9) III(6) IV(1) V(6) VI(6) S(II(7)) S(III(2))		III(1) S(III(1))	III(1)

* Fish collected in July 1976. All oocytes 0.20 mm or less were grouped together.
+ Fish collected off Japan.
S Spent ovaries; maturity stage based on diameters of the smaller oocytes.

examined for stage of maturity, 28 (56%) were either ripe (Stage VI), ripening (Stage V), or spent. These 28 fish were collected in seven different years (Table 2). The occurrence of females in ripening, ripe, and spent condition during the late spring and summer months in seven different years indicates that spawning consistently occurs during the summer. Of the three females 301 mm or longer collected in November and December, none had ovaries at Stages IV, V, or VI. Unfortunately no large females were available for examination from January through April, so whether or not spawning also occurs in these winter and spring months could not be determined.

Data on gonadal index in males and, more convincingly, on timing of recruitment of larval and small juvenile fish into the IKMT catches off Oregon, suggest that spawning is confined to the summer months. Gonadal indices were determined for male *T. macropus* 270 mm and longer collected off Oregon in different months of the year (Table 3). The highest gonadal indices occurred during the summer months. Of 21 males 270 mm or longer collected in July, August, and September, eight (38%) had a gonadal index above 6.0 and four had an index above 8.0. In eleven (50%) the index was below 5.0. Of the 11 fish examined from November through May, two (18%) had an index above 6.0, none had an index above 8.0, and nine (82%) had an index below 5.0. Not enough males were examined to determine average size at maturity, but the high gonadal index (9.3) in the

TABLE 3. Gonadal Weight and Gonadal Index (wet testes wt. /wet body wt. x 100) in Male T. macropus 271 mm S. L. or Longer Collected at Different Times of Year.

Month	Year	Fish Length (mm)	Total Wt. (g)	Testes Wt. (g)	Gonadal Index
Jan.	1962	275	34.5	2.1	6.1
Feb.	1964	286	36.0	1.5	4.2
		271	24.6	1.8	7.3+
	1967	283	35.1	1.6	4.6
Mar.	1973	300	33.0	1.5	4.5
Apr.	1962	275	24.3	0.9	3.7
May	1965	294	31.4	1.1	3.5
Jun.	1972	282	33.2	3.1	9.3+
Jul.	1967*	325	52.0	4.4	8.5*+
	1976	273	39.9	3.0	7.5+
	1977	271	32.6	0.7	2.1
		272	33.9	0.8	2.4
		296	35.2	0.5	1.4
Aug.	1966	298	42.3	3.6	8.5+
	1977	272	32.9	0.3	0.9
Sep.	1975	300	57.4	6.2	11.0+
		284	31.0	2.1	6.8
	1978	302	46.3	2.4	5.2
		326	57.5	3.6	6.3
		302	40.6	1.1	2.7
		303	38.4	2.6	6.8
		305	42.9	2.5	5.8
		294	28.2	0.3	1.1
		291	34.7	0.9	2.6
		287	54.2	2.6	4.8
		286	35.1	0.8	2.3
		285	34.4	1.3	3.8
		280	34.3	0.6	1.7
		272	31.9	0.4	1.3
Nov.	1968	333	64.0	2.6	4.1
	1965	286	37.9	1.4	3.6
	1966	282	33.1	1.0	3.0
Dec.	1966	308	46.1	1.0	2.2

* Collected off Japan. + The six highest gonadal indices.

282 mm male collected in June 1972 suggests that males of this size are probably mature.

The occurrence of larval *T. macropus* also provides information on the season of spawning. The largest collection of larval fish occurred during an August 1966 cruise that sampled far offshore from latitude 44°40'N to latitude 36°20'N (Fig. 2). One hundred thirty-one larvae were collected in twelve different hauls during this cruise (Table 4). Only a few other *T. macropus* larvae were collected in IKMT hauls, all during the summer months. In July 1975, eight larvae ranging in size from 4 to 19 mm were collected in six oblique (200 m-surface) bongo net hauls. These collections of *T. macropus* larvae during the summer months off Oregon and California are further evidence of summer spawning in this species.

From the length-frequency distributions of monthly catches of *T. macropus* off Oregon recruitment of small (50 mm-70 mm) juvenile fish apparently was seasonal, occurring consistently in the fall and winter months (Fig. 3). Small juvenile *T. macropus* were collected in the fall and winter of 1961 through 1966 and in 1972. In other years, winter sampling was minimal. The seasonal recruitment of *T. macropus* into the IKMT catch off Oregon is strong evidence that reproduction is seasonal in this species.

Spawning in *T. macropus* may be quite protracted, however, occurring over a period of several months. In mid-July 1975 small

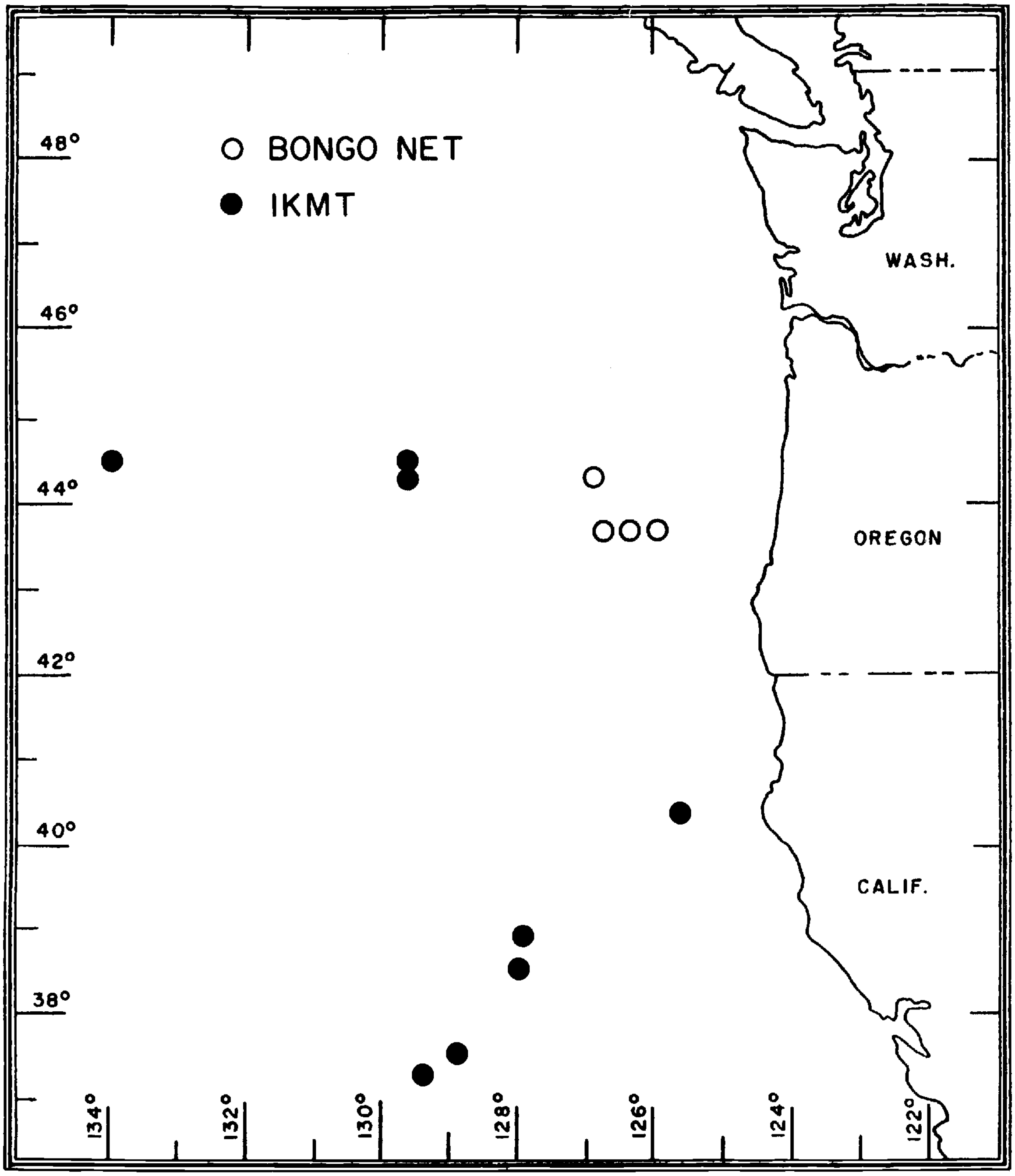


Figure 2. Collection sites of larval T. macropus off Oregon and California.

TABLE 4. Catch Data for Larval *T. macropus* Collected off Oregon and California with IKMT and Bongo Trawls During O. S. U. Cruises. Only a Very Few Other Larval *T. macropus* not Included in the Table Have Been Collected During O. S. U. Cruises.

Date	Haul	Location	Time	Depth	Number of Larvae
24/8/65	723	44-39, 130-00	0115-0205	0-200m	2
27/7/66	867	44-39, 133-54	0342-0428	0-140m	1
17/8/66	870	44-27, 129-37	2127-2243	0-75m	5
"	871	44-22, 129-33	2317-0030	surface	6
19/8/66	872	40-23, 125-30	1150-1423*	0-75m	7
"	873	40-22, 125-32	1430-1615*	surface	17
20/8/66	874	37-43, 128-46	1527-2145*	0-1000m	5
"	875	37-18, 129-20	2357-0208	0-75m	10
21/8/66	876	37-20, 129-13	0219-0358	surface	44
"	877	38-36, 127-59	1900-2010	0-75m	1
"	878	38-40, 127-57	2020-2120	surface	8
22/8/66	879	38-59, 127-53	0050-0245	0-75m	5
"	880	39-04, 127-51	0255-0436	surface	23
16/7/75	Bongo	43-40, 85+	---------	200-0m	1
"	"	43-40, 105+	---------	"	3
"	"	43-40, 125+	---------	"	1
"	"	44-20, 145+	---------	"	1

* Daytime haul

\+ Latitude followed by nautical miles from the Oregon coast.

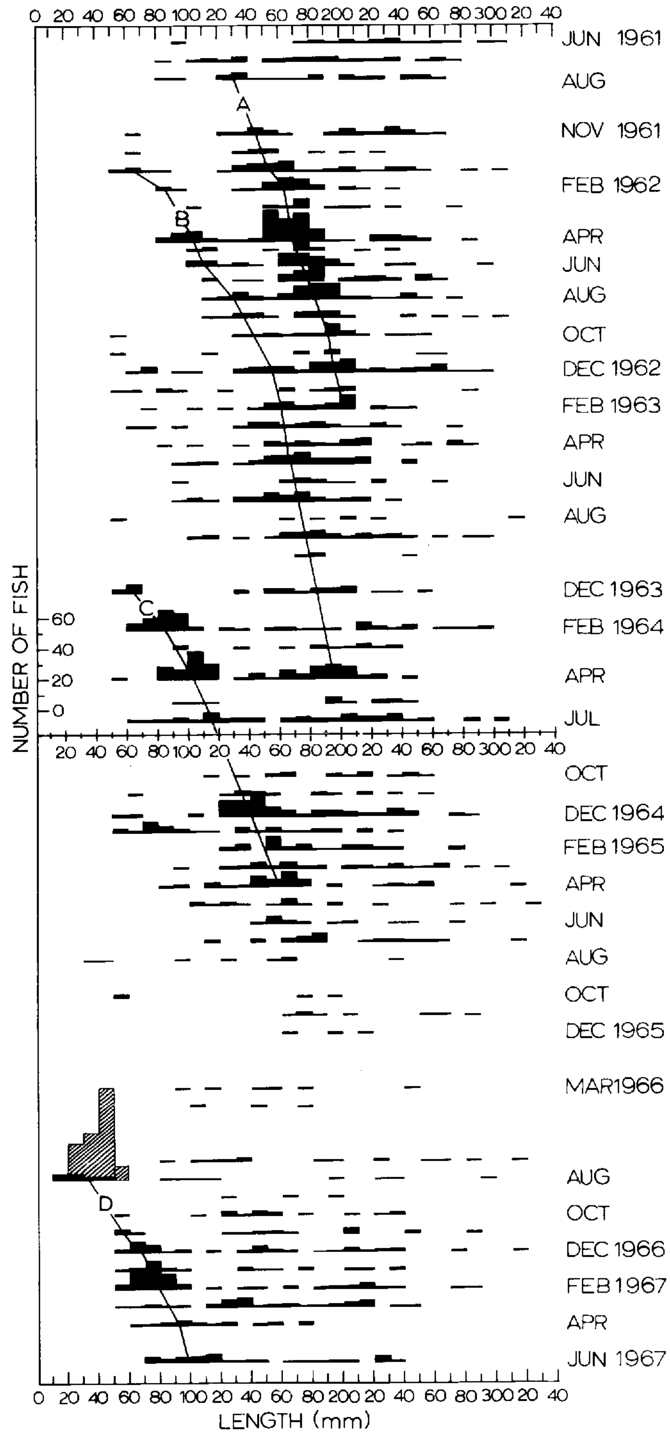


Figure 3. Length-frequency distributions of monthly catches of T. macropus off Oregon. Crosshatching in August 1966 represents larvae collected off Central California. (See Fig. 2) The time scale and scale of fish number (both vertical) are constant.

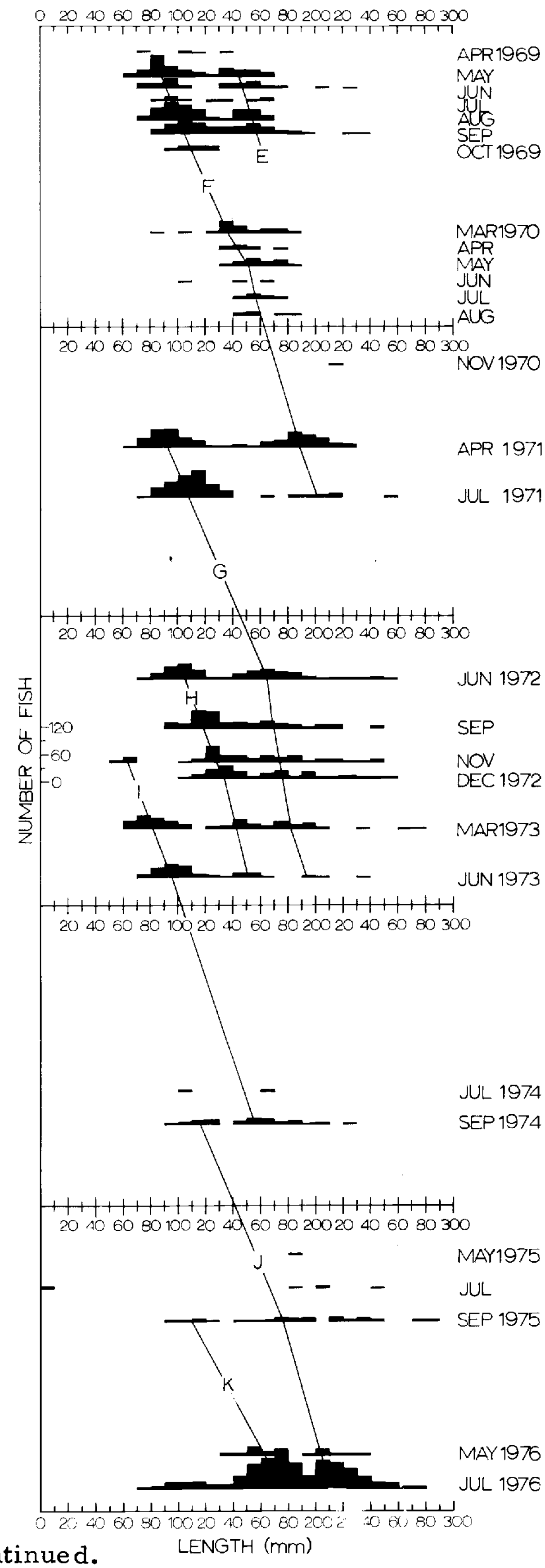


Figure 3. Continued.

(3.9 mm-19 mm) larval T. macropus were collected off Oregon in the oblique bongo net hauls. In late September of that same year a Stage V female was collected off Oregon. The presence of a female in pre-spawning condition in late September in the same year that larvae were collected in July indicates that the spawning season in this year lasted from at least July through September. The range in size of larvae collected in August 1966 also suggests that spawning may be protracted. Larvae from 17 mm to 53 mm were collected over a period of five days. This broad length range is most readily explained by protracted spawning, although differences in growth rate may have contributed to the size range. The presence of ripening, ripe, and spent females in the September 1978 catch also suggests somewhat protracted spawning (Table 2).

Metamorphosis in T. macropus appears to occur when the fish are between approximately 45 mm and 55 mm in length. Many of the larvae collected in August 1966 off Central California were between 45 mm and 50 mm; some were as long as 53 mm. Several juveniles as small as 50 mm were collected in the IKMT hauls and one juvenile collected in September 1972 was 46 mm long. The recruitment of small juveniles in the fall and winter months together with the collection of larvae in the summer months suggest that larvae metamorphose generally in the fall.

Data of other investigators are consistent with the finding that

T. macropus spawns in the summer off the West Coast of North America. Aron (1960) reported taking larval T. macropus in the Northeast Pacific during September 1957, July 1958, and August 1958. These larvae were from 15 mm to 60 mm long and were collected between approximately 35°N and 49°N. (Some of these larvae may not have been T. macropus as some of the identifications were followed by question marks.) The smallest juvenile T. macropus (45 mm - 55 mm) were collected by Aron in late September 1958 between approximately 48°N and 50°N. The smallest juvenile T. macropus (46 mm-70 mm) that Robison (1973) collected were taken in November and December. E. H. Ahlstrom (personal communication) found larval T. macropus from June through October, with most records in June, July, and August in the outer half of the CalCOFI (California Cooperative Oceanic Fisheries Investigations) pattern in the years 1951, 1952, and 1955 through 1960. He also found larval T. macropus at 27 stations during the NORPAC expedition (August 1955). The collection of a ripe female in July 1967 off Japan suggests that summer spawning occurs in the western Pacific also.

Spawning in several other mesopelagic fishes has been investigated. Fast (1960) found that in Monterey Bay, California, the myctophid Stenobrachius leucopsarus spawned from November through August. Smoker and Pearcy (1970) found that S. leucopsarus spawned from October through March off Oregon. According to Ahlstrom

(1965) the larvae of fishes with subarctic-temperate distributions, such as S. leucopsarus and Tarletonbeania crenularis, are most abundant during cold seasons of the year (winter and spring) in the CalCOFI sampling area off California. Ahlstrom (1972) found larval S. leucopsarus to be most abundant from January to June and least abundant from August to October. MacGregor (1976) reported that larvae of the gonostomatid Vinciguerria lucetia were found throughout the year with peak abundance in October in the CalCOFI sampling area off California. Clarke (1974) found evidence for both seasonal and year-round spawning among the stomiatoid fishes found near Hawaii.

That seasonal spawning occurs in certain temperate water mesopelagic fishes is not surprising as the larvae of most of these fishes are found in the near-surface waters (Ahlstrom, 1969) where seasonal fluctuations in temperature or abundance of food may affect egg and larval survival. Our data indicate that larval T. macropus are most abundant in surface waters where they are found both day and night (Table 4). Ahlstrom (1959) found S. leucopsarus larvae in greatest numbers between 24 m and 64 m depth.

T. macropus and S. leucopsarus, two mesopelagic species, the geographical ranges of which broadly overlap and the vertical distributions of which are very similar, spawn during different seasons off Oregon: T. macropus in summer and S. leucopsarus in winter. That spawning is seasonal in these two species suggests that they may be taking advantage of some seasonal condition in the environment of the upper waters that increases survival in eggs or larvae. This condition could be a seasonal maximum of food in the size range that can be captured and eaten by the larvae; a period of low abundance of predators on the larvae; a period of temperatures that promote survival; or other factors. The difference in spawning season off Oregon between these two species may be related to differences in larval diet and the abundance cycles of the food that each eats, or the difference may be related to the adaptation of the larvae to different temperature ranges; larval *T. macropus* to the relatively warm temperatures found in the summer above the seasonal thermocline offshore and larval *S. leucopsarus* to the cooler temperatures found in the winter. Studies of larval diet have not been done for either of these species.

Abundance of Larval and Adult *T. macropus* in the Catch off Oregon

Larval *T. macropus* were seldom collected in the IKMT hauls off Oregon. Although the larvae are of dimensions that would allow them to escape through the 5 mm (bar measure) mesh if they were oriented properly, that more were not collected is surprising, especially since the IKMT cod end was lined with 0.571 mm mesh plankton netting. That the IKMT is capable of collecting larval

T. macropus is evident from the large catches of larvae made with it in the upper 75 m far offshore Oregon and California in August 1966 (Table 4). Spawning in *T. macropus* may be concentrated far offshore, although the collection of 24 ripening, ripe, or spent females in five different years between approximately 65 and 80 nautical miles off the central Oregon coast, an area where much of the IKMT sampling was concentrated, suggests that some spawning also occurs in this nearer shore region.

Large *T. macropus* (251 +mm in length) were most abundant in tows to 500 m or deeper. In the IKMT hauls made between 1961 and 1976 these large fish made up 10.0% of the catch in deep tows to at least 500 m and only 2.3% of the catch in tows to 250 m or shallower. *T. macropus*, 301 +mm in length, made up 1.8% of the catch in the deep IKMT hauls and only 0.2% in the shallow hauls (Fig. 4). Similarly in tows to 210 m or shallower with a much larger pelagic trawl (approximately 65 m^2 mouth area) in July 1976, *T. macropus* 251 +mm in length made up only 3.8% and those 301 +mm in length 0.0% of the catch, while in tows to 500 m and deeper in September 1978 fish 251 +mm in length made up 29.6% and those 301 +mm in length 16.5% of the catch (Fig. 4).

The greater relative abundance of fish 301 +mm in length in deep hauls with the large net (16.5%) as opposed to deep tows with the IKMT (1.8%) suggests substantial avoidance of the IKMT by larger

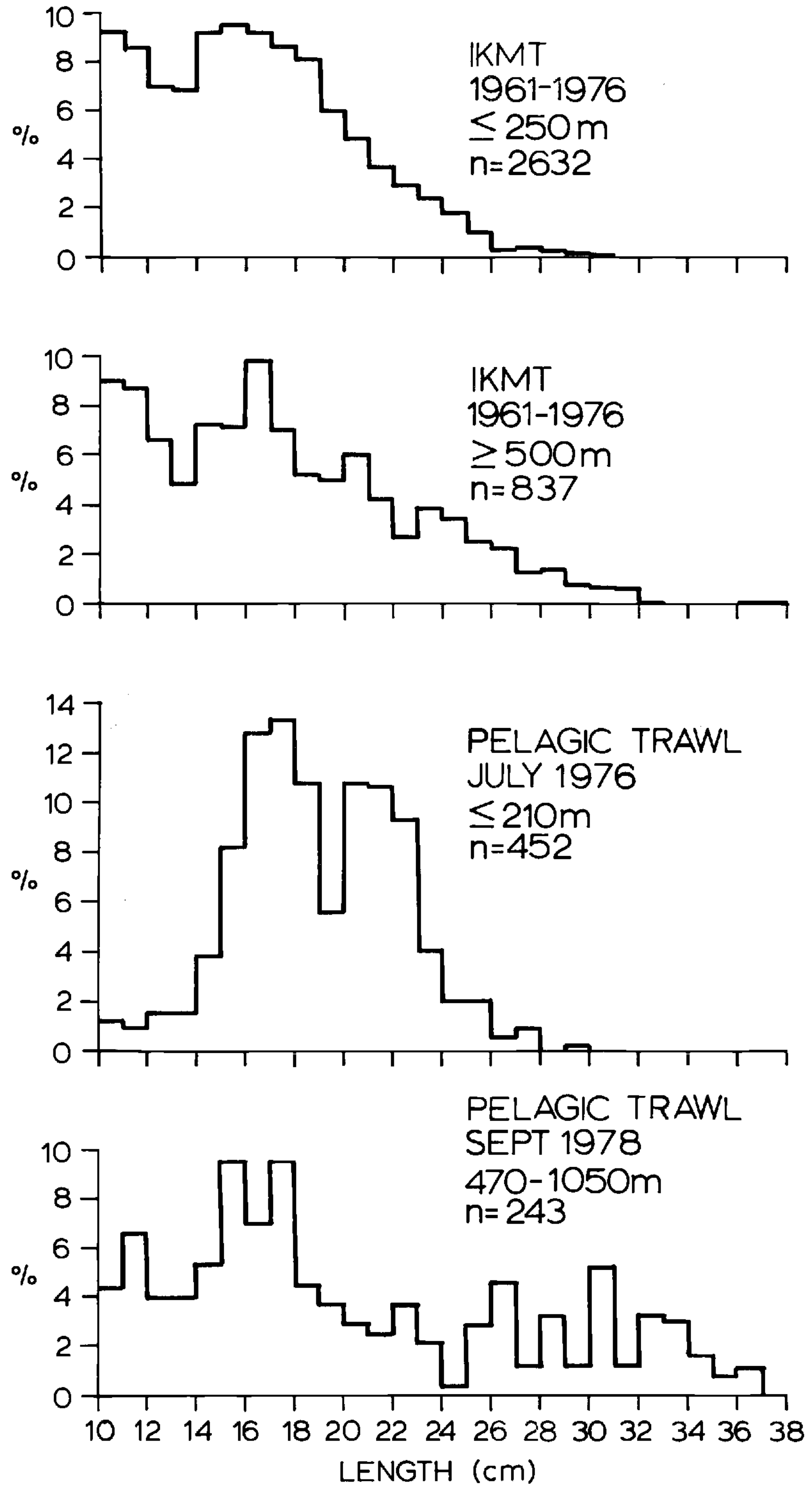


Figure 4. Length-frequency distributions of shallow and deep catches of T. macropus with the IKMT and with a much larger pelagic trawl.

fish. Net avoidance by these large fish helps explain the extremely low percentage of adult T. macropus in the IKMT catches.

The relative abundance of large fish (251 +mm) in the deep tows of both the IKMT and the large pelagic trawl is higher than in the respective shallow tows (Fig. 4). In the September 1978 collection T. macropus occurred in deep tows during both day and night. In the deep night hauls fish 251+mm made up 50.0% and those 301+ mm 28.6% of the catch, while in the deep day hauls fish 251+ mm made up 25% and those 301+ mm 13.9% of the catch. That the relative abundance of large fish in both day and night deep collections is much greater than in shallower collections and that the relative abundance these large fish increases in deep night collections suggest that unlike smaller T. macropus, large T. macropus do not migrate into the upper waters at night.

There is little evidence that net escapement by T. macropus is greater in the large pelagic trawl lined with 19 mm mesh (stretch measure) than in the IKMT lined with 5 mm mesh (bar measure). The relative abundance of smaller fish (101 mm to 200 mm) in catches with the large trawl appeared to be just as great as in catches with smaller trawls taken during the same month, with the exception of the August 1977 catch when sample sizes were low (Table 5).

The relative abundance of fish smaller than about 140 mm was low in both the May 1976 and the July 1976 catch with the IKMT

TABLE 5. Comparisons of Length-Frequency Distribution of *T. macropus* in IKMT and RMT Catches with Distributions in Large Pelagic Trawl Catches.

Cruise	Date	Depth Range	Gear	101-150mm	151-200mm	201-250mm	251-300mm	300mm+	n
Wecoma	5/76	50- 500m	5.4m^2 IKMT 9' RMT	14 16%	45 52%	26 30%	1 1%	1 1%	87
Wecoma 7607	7/76	70- 465m	"	6 15%	17 45%	15 40%	0	0	38
Pacific Raider	7/76	55- 500m	65m^2 pelagic trawl	65 12%	254 48%	184 35%	22 4%	0	525
Yaquina 7509	9/75	250- 350m	5.4m^2 IKMT	13 17%	25 33%	26 35%	9 12%	2 3%	75
Oregonian	9/75	340- 375m	65m^2 pelagic trawl	6 29%	6 29%	7 33%	1 5%	1 5%	21
Wecoma 7708	8/77	260- 325	5.4m^2 IKMT	2 10%	1 5%	5 26%	11 58%	0	19
Excaliber	8/77	490 510m	65m^2 pelagic	0	1 4%	13 48%	8 30%	5 18%	27

and RMT suggesting that the similar low abundance of these small fish in the catch made with the large pelagic trawl in July 1976 was due not to net escapement but to low abundance of these smaller fish at the time of sampling.

Growth

Length-Frequency Analysis

The smallest juvenile *T. macropus* (50-70 mm) were consistently recruited into the catches in the fall and winter months (Fig. 3). In most years recognizable modes were formed as these small fish were recruited. With time the position of these modes shifted. This suggested that major modes in monthly catches of *T. macropus* likely represented year-classes, and the progressions with time of these modes should represent average growth of surviving fish until sizes are reached at which net avoidance occurs. The catches typically contained two to three distinct modes.

Progressions of 11 modes are indicated by lines A through K in Figures 3A and 3B. Data discussed in the section on reproduction indicate that spawning occurs during the summer months. Small juvenile *T. macropus* recruited in the winter months probably hatched the preceding summer and metamorphosed that fall or early winter, in which case progressions B, C, D, F, G, and I would represent the 1961, 1963, 1966, 1968, 1970, and 1972 year-classes, respectively. As progression A is composed of larger fish than progression B it probably represents the preceding (1960) year-class. Similarly progression E to the right of F probably represents the 1967 year-class while progression H in between progressions G (1970) and I (1972) probably represents the 1971 year-class. Progressions J and K to the left of progression I probably represent the 1973 and 1974 year-classes, respectively. The lack of a recognizable progression between the 1968 year-class (F) and the 1970 year-class (G) suggest that the 1969 year-class may have been small. Growth curves for all eleven year-classes, based on the positions of the year-class modes in different months, are plotted together in Figure 5. As spawning in T. macropus generally occurs sometime during the summer or early fall, July has been taken as the anniversary month. Growth curves of the different year-classes are fairly similar. Among the year-classes the range in average fish length in the first January following hatching was 65 to 75 mm, at one year 95 to 125 mm, at two years 150 to 175 mm, at three years 195 to 215 mm. The similarity of the eleven growth curves suggests uniformity among years in factors affecting growth and timing of spawning in T. macropus.

Modal progressions generally could not be followed past about 200 mm, when the fish were approximately three years old. Catches of larger fish with the IKMT nets were generally quite low and

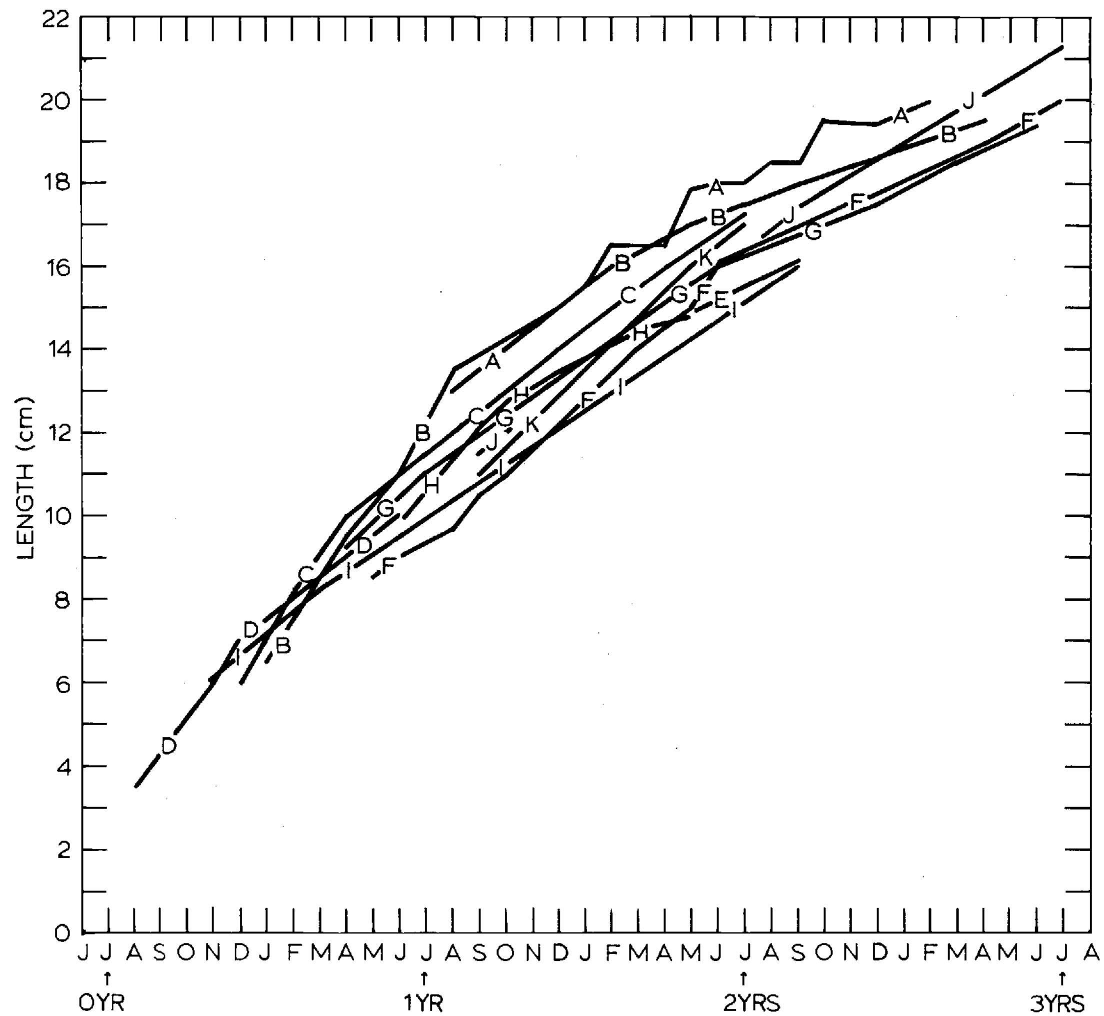


Figure 5. Growth curves for eleven year-classes of T. macropus, based on the positions of the year-class modes in different months. July was chosen as the anniversary month.

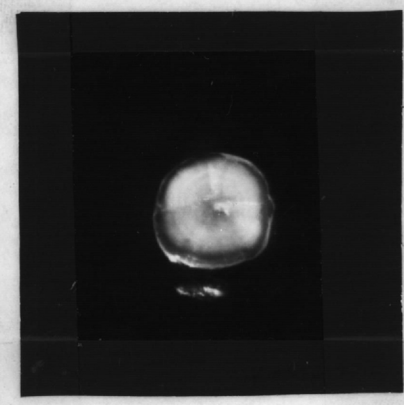
distinct modes were not apparent.

Otolith Analysis

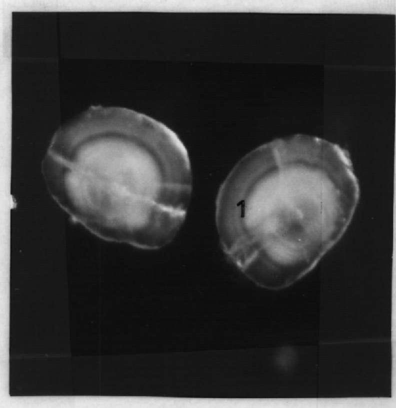
Approximately 50 percent of the otoliths could be interpreted; the others showed a complicated ring structure with thin, faint rings that formed indistinct "annuli."

Photographs of five T. macropus otoliths (Fig. 6) show that hyaline zones (dark under reflected light) were generally much narrower than the opaque zones (white). The centers of the otoliths were opaque, but occasionally would appear slightly hyaline when examined in glycerin or water (Fig. 6B). In temperate water deposition of the hyaline zone is often associated with periods of slow growth during the winter months. Often one hyaline and one opaque zone are deposited each year (Williams and Bedford, 1974). Most studies of growth employing otoliths have been of freshwater species or marine species living on or above the continental shelf. Growth in mesopelagic fish species has seldom been studied and whether their otoliths follow the same general pattern of zone formation as other temperate water fishes is uncertain.

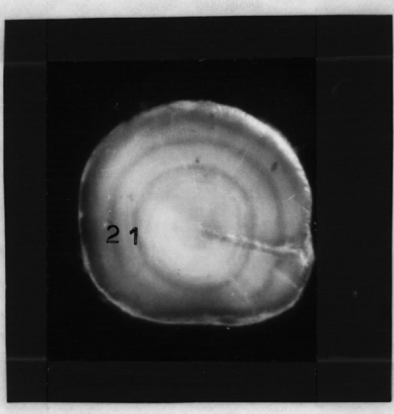
To determine the season in which the hyaline zone is deposited, the margins of otoliths from fish collected in all seasons should be examined. For the present study, however, only otoliths from May, July and September were available for examination, so to determine



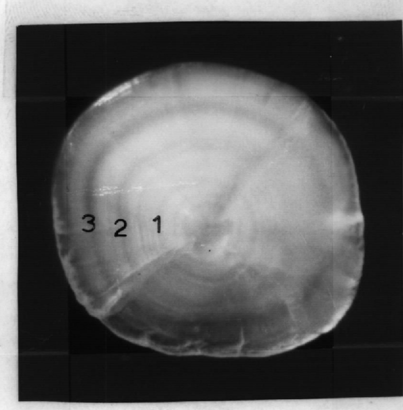
A. July 1976, 65 mm S. L.
< 1 Year



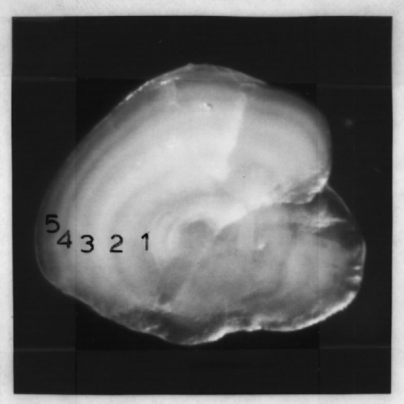
B. May 1976, 101 mm S. L.
1 Year



C. July 1976, 176 mm S. L.
2 Years



D. Sept. 1974, 235 mm S. L.
3 Years



E. May 1976, 231 mm S. L.
5 Years

Figure 6. Photographs of five otoliths from T. macropus showing annuli.

when the hyaline ring is deposited was not possible. The margins of the otoliths collected in May and July appeared hyaline as often as they appeared opaque (Table 6), although determining whether the margin was opaque or hyaline was often difficult. The percentage of hyaline margins was quite high in the September otoliths, although the sample size was low. Otoliths from one small fish collected in July had a distinctly hyaline margin (Fig. 6A).

Smoker and Pearcy (1970) found that the percentage of translucent (hyaline) margins was greatest from November through February and lowest in the summer in otoliths of the mesopelagic myctophid fish Stenobrachius leucopsarus. Ninety-five percent of the 38 S. leucopsarus otoliths they examined from November 1965 had hyaline margins. As S. leucopsarus and T. macropus are both found in the same depth range and smaller individuals of both undertake diel migrations into the near surface waters (Pearcy et al., 1977), both species probably experience some of the same environmental fluctuations (such as temperature change) that might cause the shift from deposition of opaque material to hyaline material in the otolith.

In interpreting the otoliths of T. macropus, it was assumed that the hyaline zone, like that in S. leucopsarus, is deposited sometime in the fall or winter. The opaque center of each T. macropus otolith would then represent growth in the summer of the year in which the fish hatched, the first hyaline ring would be deposited sometime that

TABLE 6. Appearance of Otolith Margins.

Date		n	Hyaline	Opaque	Hyaline and Opaque
May	1976	62	37%	41%	26%
July	1976	38	36%	32%	32%
September	1974, 1975	9	78%	22%	---

late summer, fall or winter, and opaque material would be deposited from winter or spring through the summer. If this is the pattern of ring formation in otoliths of T. macropus then age in years of a fish collected in the summer would be equal to the number of internal hyaline rings (annuli) in its otolith.

This assumption was made for aging 78 T. macropus collected in May and July 1976. In Figure 7 the length range of each age group as determined by otolith analysis is plotted together with the length-frequency distribution of the total catch of T. macropus for these two months. Although there is a fair amount of overlap, the age groups coincide fairly well with the modes in the total catch. The second and third mode each appear to be made up of three year-classes, however. Thus, the size ranges within age groups (130 to 280 mm in the two year olds, for example) as determined from otolith analysis are large and greater than expected from the length-frequency distribution of the catch. Errors in aging the fish probably contributed to the large size ranges within age groups. In some instances false annuli may have been interpreted as true annuli resulting in an over-estimation of age; in other instances the annuli may have been so thin and faint that they were overlooked resulting in an underestimation of age.

Different growth rates in males and females may also have contributed to the large length ranges within year-classes. The

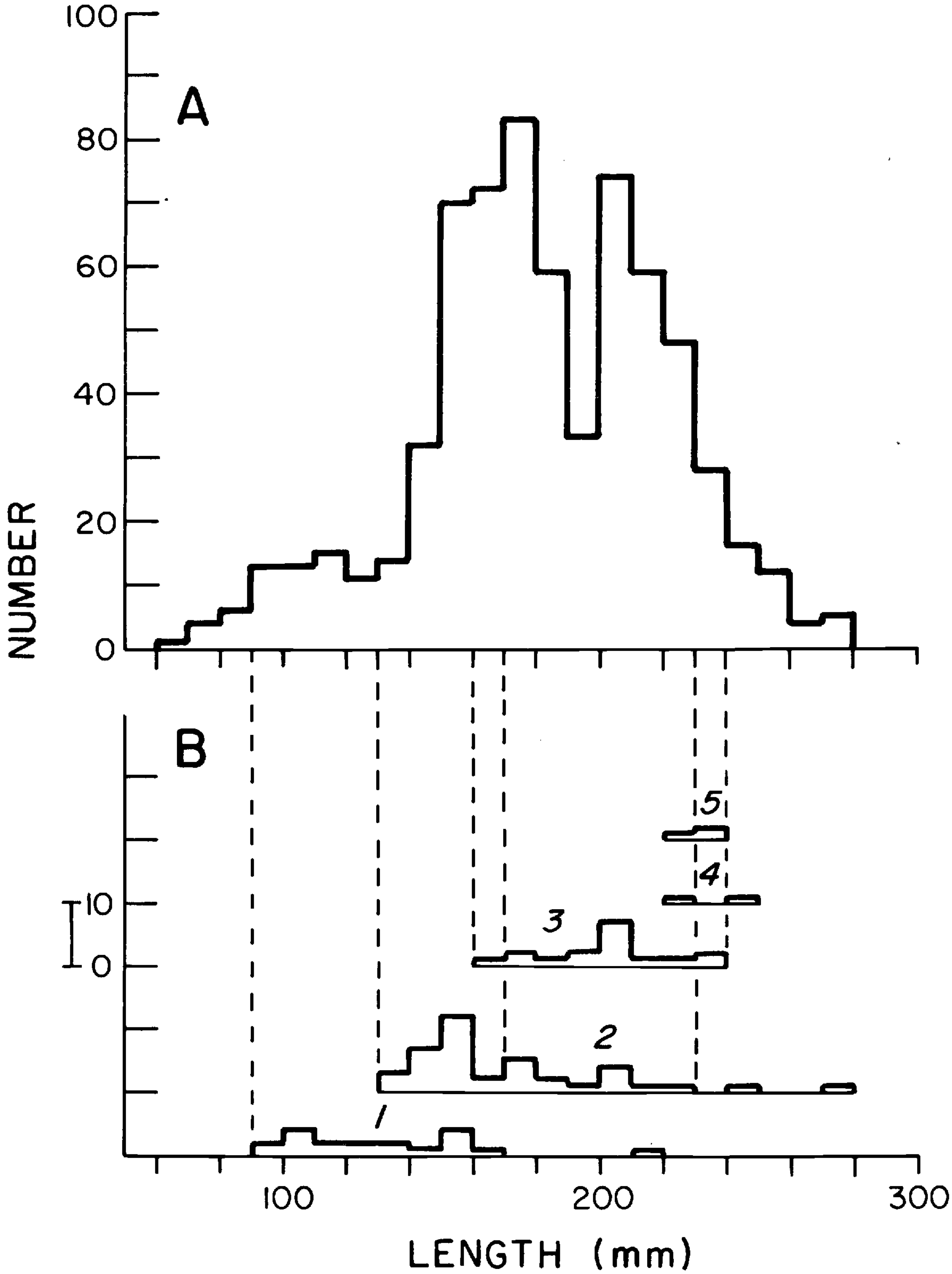


Figure 7. Length-frequency distribution of the combined May and July 1976 catch (A) compared to the length-ranges of age groups as determined by otolith analysis (B).

length-frequency distributions of male and female fish collected in July 1976 were very similar although 12% of the catch of females and only 4% of the catch of males was greater than 230 mm (Figs. 8A, 8B). In the September 1978 catch, 30.2% of the females and only 6.0% of the males were 301 mm or longer (Figs. 8A, 8B). This suggests that females grow to larger size than males. The largest specimen (382 mm) collected off Oregon in O.S.U. IKMT trawls was a female. The largest male from these hauls was 333 mm long. Although the average growth rates of males and females may be different when they are large, the similar length-frequency distributions of males and females in the July 1976 catch and the similar position of the first mode for both sexes in the September 1978 catch suggest that the growth rates are probably similar when the fish are smaller. Unfortunately, only a few of the otoliths with a readible structure came from fish that had been sexed.

Robison (1973) examined growth in T. macropus using otoliths. His results are similar to mine. He found four hyaline rings in T. macropus from 196 to 242 mm, five hyaline rings in fish from 210 to 261 mm, six hyaline rings in fish 238 and 293 mm, seven hyaline rings in a 339 mm fish and at least eight hyaline rings in a 382 mm fish.

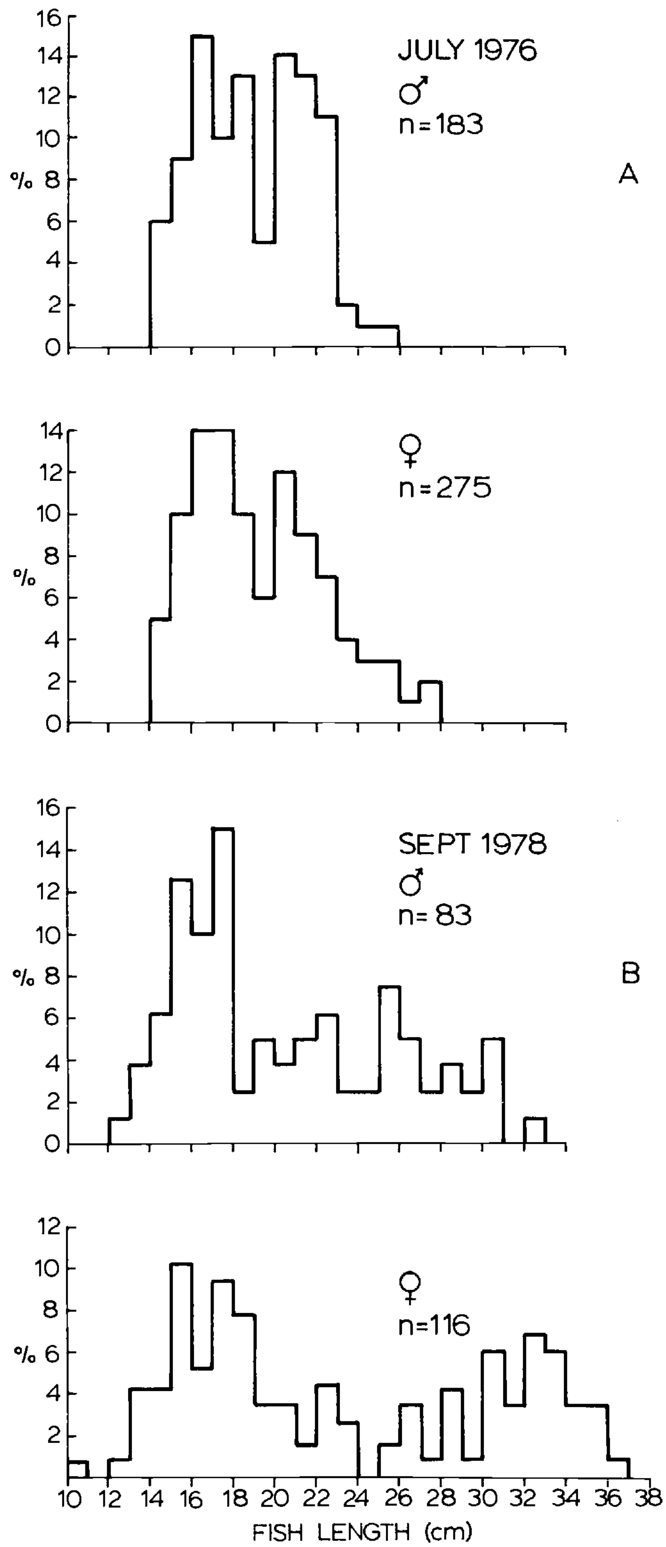


Figure 8. Size-frequency distributions of males and females for the July 1976 catch and the September 1978 catch.

Back Calculation of Age

Fish length (preserved) was found to be related to greatest otolith diameter by the relationship:

$$\text{Standard length} = 258.39 \text{ (otolith diameter)} - 25.0$$

$$n = 144, \; r^2 = .87 \;\; \text{(Fig. 9)}.$$

Using this relationship fish lengths at the time of formation of each of the internal hyaline rings were estimated in 80 otoliths (Table 7).

Comparison of the Three Methods of Aging

Growth curves derived from length-frequency analysis, from direct aging by otoliths and from back calculation from otoliths are compared in Figure 10. In positioning the back calculated curve, hyaline ring deposition was assumed to occur in November and each back calculated length is plotted above November. Growth curves derived by direct otolith aging and by length-frequency analysis are most similar. The back calculated curve falls below the other two curves, perhaps because of incorrect positioning of the back calculated curve. For example, hyaline ring deposition may begin earlier in the year than November (see Fig. 6A).

Another possibility is that hyaline deposition begins progressively earlier each year as the fish grows. This would mean that the hyaline rings are not a full year apart. A progressive delay with age

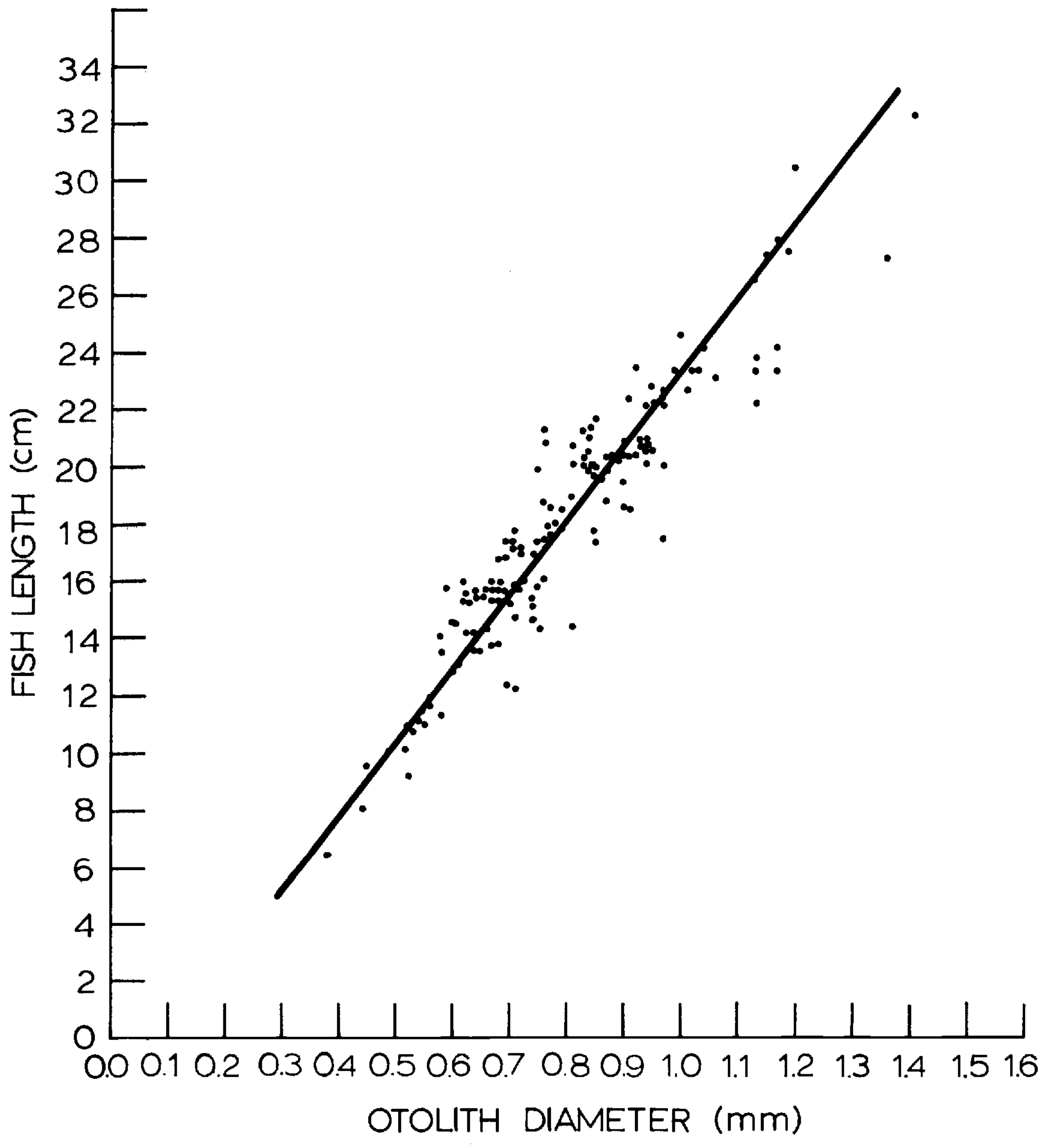


Figure 9. Fish length vs. otolith diameter.

TABLE 7. Mean Back Calculated Fish Lengths at Times of Formation of Hyaline Rings.

	n	X	SD
1st ring	80	61 mm	9.8
2nd ring	62	113 mm	23.2
3rd ring	23	161 mm	17.3
4th ring	5	187 mm	23.3
5th ring	3	206 mm	29.0

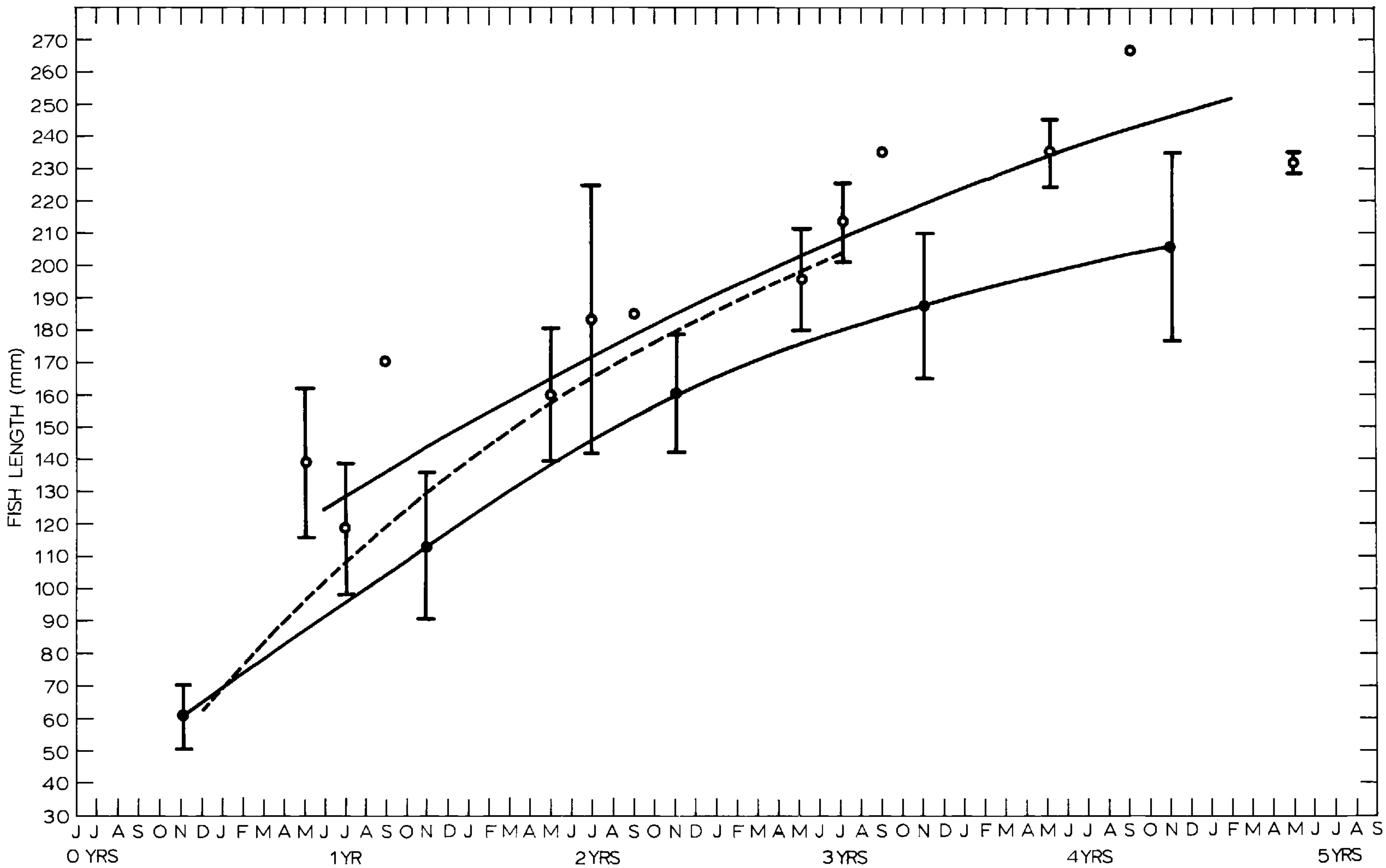


Figure 10. Growth curves of T. macropus derived from length-frequency analysis, from direct aging with otoliths and from back calculation from otoliths. Open circles are mean fish lengths at different ages as determined by direct aging with otoliths. Closed circles are mean back calculated fish lengths at the time of formation of each of the hyaline rings. The vertical lines indicate ± one standard deviation.

in the onset of hyaline ring formation is known to occur in the North Sea and Arctic cod (Williams and Bedford, 1977). Scott (1973) suggested the possibility that resorption of the otolith margin may occur at the time of hyaline ring formation in the northern sand lance (Ammodytes dubius). If resorption occurs in T. macropus otoliths, the relationship between fish length and otolith diameter would be variable. During the period of resorption, the otolith diameter in a fish of given length would be smaller than in the period immediately before resorption. Thus, if resorption of the otolith margin occurred, the relationship between fish length and otolith diameter based on fish collected in May, July, and September (Figure 9) may not have been entirely appropriate for use in predicting fish length at the time of annulus formation.

Age at Maturity

The average growth rate between two and three years of age was about 30-40 mm per year as estimated from length-frequency analysis and direct otolith aging. If growth continued at this rate, the average age at 300 mm (the approximate size of maturity in females) would be about six years.

Weight-Length Relationships

The relationship between fish length and the logarithm of wet weight was found to be slightly curvilinear. By breaking the data into two groups each could be approximated by a straight line. The relationship of weight to length for fish from about 50 mm to about 220 mm was:

$$Wt = (5.4 \times 10^{-7})\ (\text{length})^{3.08}$$
$$n = 88,\ r^2 = .99,$$

where weight is in grams and length in mm. As the exponent is almost exactly 3.00, growth between 50 and 220 mm is practically isometric; that is, the body shape of the fish does not change with increases in length. Between 220 and 382 mm the relationship between weight and length was:

$$Wt = (1.1 \times 10^{-9})\ (\text{length})^{4.27}$$
$$n = 99,\ r^2 = .86.$$

As the exponent is larger than 3.00, fish larger than 220 mm became progressively heavier bodied with increase in length.

Feeding Habits

Diet and Changes in Diet with Growth

Nineteen prey taxa were identified from *T. macropus* stomachs (Table 8). Among smaller juvenile *T. macropus* (51-100 mm) euphausiids (principally *E. pacifica*) were by far the most frequently occurring food item, appearing in 90 percent of stomachs with food

TABLE 8. Frequencies of Occurrence of Food Items in *T. macropus* Stomachs. For Each Food Item the Number and Percentage of Stomachs Containing Food in Which it Occurs Are Given.

	All Lengths	*T. macropus* Lengths 51-100 mm	101-150 mm	151-200 mm	201-250 mm	250 mm+
No. of stomachs examined	530	71	140	188	99	32
No. of stomachs with food	222	50	81	58	19	14
% of stomachs with food	42%*	70%	58%	31%	19%*	44%*
EUPHAUSIIDS (all species)	153 (69%)	45 (90%)	63 (78%)	37 (64%)	5 (26%)	3 (21%)
Euphausia pacifica	122 (55%)	32 (64%)	58 (72%)	27 (47%)	3 (16%)	2 (14%)
Thysanoessa spinifera	5 (02%)	1 (02%)		4 (07%)		
T. longipes	3 (01%)	2 (04%)			1 (05%)	
Nematoscelis gracilis	2 (01%)		1 (01%)	1 (02%)		

TABLE 8. Continued

	All Lengths	*T. macropus* Lengths 51-100 mm	101-150 mm	151-200 mm	201-250 mm	251 mm+
N. difficilis	1 (01%)			1 (02%)		
Unidentified euphausiids	37 (17%)	18 (36%)	11 (14%)	6 (10%)	1 (05%)	1 (07%)
DECAPODS						
Sergestes similis	30 (14%)		4 (05%)	17 (29%)	7 (37%)	2 (14%)
MYSIDS						
Boreomysis sp.	1 (01%)				1 (05%)	
AMPHIPODS						
Vibilia spp.	1 (01%)				1 (05%)	
Cyphocaris challengeri	1 (01%)			1 (02%)		
COPEPODS						
(all species)	6 (03%)	3 (06%)	2 (02%)	1 (02%)		
Calanus spp.	2 (01%)	2 (04%)				

TABLE 8. Continued

	All Lengths	*T. macropus* Lengths 51-100 mm	101-150 mm	151-200 mm	201-250 mm	251 mm+
Unidentified copepods	4 (02%)	1 (02%)	2 (02%)	1 (02%)		
Unidentified crustacean fragments	5 (02%)	2 (04%)	1 (01%)	1 (02%)		1 (07%)
FISH (all species)	38 (17%)	2 (04%)	8 (10%)	10 (17%)	7 (37%)	11 (79%)
Stenobrachius leucopsarus	5 (02%)			2 (03%)	2 (11%)	1 (07%)
S. nannochir	1 (01%)					1 (07%)
Diaphus theta	2 (01%)				1 (05%)	1 (07%)
Tarlentobeania crenularis	2 (01%)					2 (14%)
Protomyctophum thompsoni	1 (01%)					1 (07%)
Sebastes spp.	4 (02%)			3 (05%)	1 (05%)	
melamphid	1 (01%)			1 (02%)		

TABLE 8. Continued

	All Lengths	*T. macropus* Lengths 51-100 mm	101-150 mm	151-200 mm	201-250 mm	251 mm+
Unidentified fish	22 (10%)	2 (04%)	8 (10%)	4 (07%)	3 (16%)	5 (35%)
MOLLUSCS						
Pteripods	1 (01%)			1 (02%)		
Squids	1 (01%)			1 (02%)		
Unidentified material	5 (02%)	1 (02%)	4 (05%)			

* Includes fish examined because their stomachs obviously contained food; therefore the sample is not random.

(positive stomachs). Copepods, the second most frequently occurring food item were found in only six percent of the positive stomachs. No taxa occurred in as great numbers per stomach as did euphausiids (which averaged 1.9 per stomach) (Table 9). Many small T. macropus had stomachs full of euphausiids. The diet of those T. macropus 101-150 mm long was quite similar to that in the smaller fish. Euphausiids were again the most frequently eaten prey occurring in 78 percent of positive stomachs, with E. pacifica occurring in 72 percent, and again they occurred in the greatest numbers per stomach (2.3). Fish were the second most frequently eaten prey, appearing in ten percent of stomachs, followed by the pelagic shrimp Sergestes similis (5%). In the 151 to 200 mm length group, euphausiids occurred most frequently (64 percent) followed by Sergestes similis (29 percent) and fish (17 percent). In the 201 to 250 mm length group euphausiids occurred only in 26 percent of stomachs while fish (Stenobrachius leucopsarus, Diaphus theta, Sebastes and unidentifiable remains) and Sergestes similis both occurred in 37 percent of positive stomachs. In the 251 mm+ length group, fish (myctophids and unidentifiable remains) occurred in 79 percent of positive stomachs while euphausiids occurred in only 21 percent and Sergestes similis in 14 percent.

The increase in frequency of occurrence of fish and Sergestes similis in stomachs of larger T. macropus suggests that these taxa

TABLE 9. Mean Numbers Per Stomach and Ranges in Numbers Per Stomach of Three Food Taxa for Different Length Groups of *T. macropus*.

	Euphausiids		*Sergestes similis*		Fish	
	$\bar{x}$	R	$\bar{x}$	R	$\bar{x}$	R
51-100 mm	1.9	1-5	---	---	1.0	1
101-150 mm	2.3	1-7	1	1	1.0	1
151-200 mm	1.7	1-4	1.2	1-3	1.0	1
201-250 mm	1.2	1-2	1.1	1-2	1.1	1-2
251 mm+	1.0	1	1.5	1-2	1.1	1-2

become increasingly important in the diet of the larger fish. Euphausiids are less important in the diet of the large fish (200 mm) than in the smaller fish as indicated both by the decrease in frequency of occurrence and number per stomach (Tables 8 and 9). If, as the fish grew they continued to feed heavily on euphausiids the number of euphausiids per stomach would be expected to increase as the capacities of the stomachs increased; however, no large _T. macropus_ were found with more than two euphausiids in the stomach.

Frequencies of occurrence of prey taxa in intestines appear in Table 10. Intestinal contents should be less subject to effects of possible net feeding than stomach contents, therefore, comparison of intestinal contents with stomach contents is important in determining the reliability of stomach contents as indicators of natural diet. As in the stomachs, euphausiids were the most frequently occurring prey in the intestines of small _T. macropus_. The frequency of occurrence in intestines of euphausiids decreased in the larger fish, however, the decline was not as sharp as in the stomachs. Smaller _T. macropus_ had fairly high percentages of unidentifiable crustacean exoskeleton parts in their intestines and some of these may have been euphausiids. As in the stomachs, frequency of occurrence of _Sergestes_ was low in small _T. macropus_ and higher in the larger _T. macropus_ up to 250 mm. Fish were found in low percentages of the intestines, the highest percentage occurring in the

TABLE 10. Frequencies of Occurrence of Food Items in T. macropus Intestines. For Each Food Item the Number and Percentage of Intestines Containing Food in Which it Occurs are Given.

	T. macropus Length Groups				
	51-100 mm	101-150 mm	151-200 mm	201-250 mm	251 mm+
No. of intestines examined	66	124	178	92	23
No. of intestines with food	17	43	54	24	5
% of intestines with food	26%	35%	30%	26%	22%
EUPHAUSIIDS (all species)	10 (59%)	21 (49%)	25 (46%)	10 (42%)	---
Euphausia pacifica	2 (12%)	11 (26%)	15 (28%)	7 (29%)	---
Unidentified euphausiids	7 (41%)	10 (23%)	10 (19%)	4 (17%)	
DECAPODS					
Sergestes similis	---	1 (02%)	8 (15%)	6 (25%)	1 (20%)

TABLE 10. Continued

	T. macropus Length Groups				
	51-100 mm	101-150 mm	151-200 mm	201-250 mm	251 mm+
COPEPODS	1 (17%)	1 (02%)	---	---	---
Unidentified crustacean remains	3 (18%)	11 (26%)	9 (17%)	---	---
FISH	---	3 (07%)	2 (04%)	3 (13%)	---
Unidentified material	4 (24%)	5 (11%)	11 (20%)	7 (29%)	4 (80%)

201-250 mm length group (13 percent). The low frequency of occurrence of fish in the intestines of even the larger *T. macropus* may have been the result of fairly complete digestion of fish material before it entered into the intestine making it hard to identify. Fish were well digested in 21 of the 38 stomachs in which they occurred. The occurrence of well digested fish in stomachs suggests that these fish were not fed on in the net and that fish are indeed part of the natural diet of *T. macropus* even though the percentage of fish in the intestines was low. Unidentifiable material occurred quite frequently in the intestines of all length groups. Taking into account the greater difficulty of identifying well-digested food in the intestines the diets as inferred from intestinal contents are similar to those inferred from stomach contents.

The percentage of stomachs containing food decreased from 70% in the 51-101 mm length group to 19% in the 201-250 mm length group. The high frequency of empty stomachs among larger fish suggest that they may feed less frequently or have faster digestion rates than the smaller fish. Well digested food was sometimes found in the esophagus suggesting vomiting of prey, however evidence for vomiting was just as frequent among smaller fish as in larger fish.

The average total length of *E. pacifica* found in stomachs of *T. macropus* 51-101 mm long was 13.1 mm, and in fish 101-150 mm the average was 13.5 mm. These small *T. macropus* were therefore feeding mainly on prey that were from 10 percent to 25 percent of their own body lengths. The fish found in stomachs of *T. macropus* 151-200 mm long averaged approximately 39 mm, those found in 201-250 mm *T. macropus* averaged 54 mm and those found in 251 mm and longer *T. macropus* averaged 65 mm. These larger *T. macropus* were feeding on prey which were approximately 20-27 percent of their body lengths, indicating their ability to catch and consume large prey. The large fish also fed on smaller organisms such as euphausiids and sergestids. Although the average size of largest prey increased with the size of *T. macropus*, the ratio of prey length to *T. macropus* length over the size range studied was always between approximately 1:10 and 1:4.

Osterberg et al. (1964) examined the stomachs of 52 specimens of *T. macropus*. They found that euphausiids and sergestids occurred most frequently, but about one-half of the total volume of stomach contents was composed of myctophids. Robison (1973) found in 45 *T. macropus* stomachs containing food, fish remains in 48 percent and zooplankton remains in 38 percent. Neither paper, however, gave the size of *T. macropus* examined.

Comparison of Diet in *T. macropus* with that in Three Myctophid Fishes

Euphausiids were the most important food category in the diets of *S. leucopsarus*, *D. theta*, and *T. crenularis* (Tyler and Pearcy, 1975) as well as in small (51-150 mm) *T. macropus*. Thus, small *T. macropus* occupy a similar trophic level and are possible competitors for food with these myctophids. *E. pacifica* is the single most important prey species in the diets of the three myctophids and small *T. macropus*. Copepods were important in the diets of the myctophids but occurred very infrequently in the *T. macropus* 51 mm and longer.

Seasonality in Diet

Euphausiids (mainly *E. pacifica*) were usually the most frequently occurring food in stomachs from small *T. macropus* (51-150 mm) collected at different times of year (Table 11). Exceptions were September 1972 and 1975 when fish occurred in high frequencies in the stomachs, suggesting that at certain times (or places) fishes or other non-euphausiid taxa can be important in the diet of small *T. macropus*. Among the larger *T. macropus* (151-200 mm) diet also appears to be rather similar during different times of year. Larger fish (201+ mm) showed most variability in composition of diet, perhaps a result of small sample sizes.

Diel Periodicity in Feeding

There was little evidence for diel periodicity of feeding in

TABLE 11. Frequencies of Occurrence of Three Food Taxa in *T. macropus* Stomachs for Different Length Groups and Cruises. First Two Digits of Cruise Numbers Give the Year; the Last Two the Month.

Cruise	7302	7104	7206	7607	7209	7211
51-100 mm *T. macropus*						
No. stomachs examined	23	17	1	17	6	7
No. with food	13	15	0	11	4	7
% of stomachs with food	57%	88%	0%	65%	67%	100%
Euphausiids	100%	93%	---	91%	25%	100%
Sergestes similis	---	---	---	---	---	---
Fish	---	---	---	---	50%	---
All other taxa	08%	13%	---	09%	50%	---

Cruise	7302	7104	7206	7607	7209	7509	7211
101-150 mm *T. macropus*							
No. stomachs examined	7	7	4	32	45	2	43
No. with food	3	7	0	21	14	2	34
% of stomachs with food	43%	100%	0%	66%	31%	100%	79%
Euphausiids	67%	100%	---	90%	36%	---	85%

continued

TABLE 11. Continued

101-150 mm *T. macropus*, continued

Cruise	7302	7104	7206	7607	7209	7509	7211
Sergestes similis	---	---	---	---	---	---	12%
Fish	---	---	---	---	43%	100%	---
All other taxa	33%	---	---	05%	21%	---	03%

Cruise	7302	7104	7206	7607	7209	7509	7211	other*
			151-200 mm *T. macropus*					
No. stomachs examined	15	8	5	96	25	3	32	4
No. with food	3	5	0	30	8	2	7	4
% stomachs with food	20%	63%	0%	31%	31%	67%	22%	100%
Euphausiids	67%	40%	---	77%	38%	50%	57%	50%
Sergestes similis	33%	---	---	20%	50%	50%	43%	50%
Fish	---	20%	---	17%	38%	---	14%	---
All other taxa	33%	14%	---	07%	---	---	---	---

TABLE 11. Continued

Cruise	7302	7104	7607	7209	7509	7211	other*
			201-250 mm T. macropus				
No. stomachs examined	3	3	55	17	4	15	2
No. with food	0	0	11	3	2	1	2
% of stomachs with food	0%	0%	20%	18%	50%	7%	100%
Euphausiids	---	---	36%	---	---	---	50%
Sergestes similis	---	---	36%	67%	---	100%	---
Fish	---	---	36%	---	100%	---	50%
All other taxa	---	---	---	33%	---	---	50%

TABLE 11. Continued

Cruise	7302	7607	7707	7209	7211	other*
			251 mm+ *T. macropus*			
No. stomachs examined	3	12	7	1	1	8
No. with food	0	2	4	0	0	8
% of stomachs with food	0%	17%	57%	0%	0%	100%
Euphausiids	---	---	75%	---	---	---
Sergestes similis	---	---	25%	---	---	13%
Fish	---	50%	75%	---	---	88%
All other taxa	---	50%	---	---	---	---

* Fish from assorted cruises used in reproduction study and examined because stomach appeared to contain food.

T. macropus. The percentages of stomachs at each stage of fullness and each stage of digestion show no clear trend between night and day hauls (Table 12). Among the smaller *T. macropus* (51-150 mm) euphausiids occurred with similar frequency day and night.

Daytime hauls between 400-500 m caught 27 *T. macropus* with a total of 45 *E. pacifica* in their stomachs. In some of these hauls few *E. pacifica* were collected in the net. The center of the daytime depth range of *E. pacifica* in the transition waters of the California Current (Brinton, 1967; Youngbluth, 1976) and in subarctic waters (Marlowe and Miller, 1975) is between 200 and 400 or 500 meters. If the daytime range of *E. pacifica* is mainly above 400 meters off Oregon then these *T. macropus* caught below 400 meters most likely fed on *E. pacifica* at a shallower depth sometime previous to being collected. Slow digestive rate with retention of food in the stomach for most of a day would mask periodicity in feeding and this may be occurring in *T. macropus*. The data, however, give no convincing evidence for diel periodicity in feeding and suggest, in the absence of better data on the depth distribution of *E. pacifica* off Oregon that feeding is aperiodic.

Geographical Distribution

Tactostoma macropus has been collected extensively in the North Pacific Ocean (Fig. 11). Its range off the coast of North

TABLE 12. Frequencies of Occurrence of Food Items in Stomachs for Different Length Groups of T. macropus and Different Times of Day. Night Includes Morning and Evening Twilight.

Cruise	Length Group	Time	No. of stomachs examined	No. with food	% with food	% S.F. 0	% S.F. 1	% S.F. 2	% S.F. 3	% S.D. 1	% S.D. 2	% S.D. 3	EUPHAUSIIDS (total)	E. pacifica	Other or unident. euphausiids	FISH	Sergestes similis	All other taxa combined and unidentified material
All cruises combined	51-150mm	N	147	88	60%	40%	18%	20%	21%	19%	44%	47%	82%	67%	28%	10%	0%	11%
		D	63	43	68%	32%	16%	33%	19%	35%	56%	26%	84%	74%	23%	02%	07%	07%
Pacific Raider (7607)	51-150mm	N	10	7	70%	30%	20%	40%	10%	43%	57%	14%	100%	100%	14%			
		D	39	25	64%	36%	15%	36%	13%	44%	52%	36%	88%	88%	20%			08%
	151-200mm	N	77	21	27%	73%	16%	08%	04%	48%	38%	29%	67%	62%	10%	24%	14%	10%
		D	19	9	47%	53%	26%	21%	0%	44%	56%	22%	89%	89%	22%		33%	
	201-250mm	N	42	6	14%	86%	12%	0%	02%	33%	17%	50%	33%	0%	33%	33%	33%	
		D	12	5	42%	58%	25%	0%	17%	60%	20%	20%	40%	40%	0%	60%	20%	
	251mm+	N	4	1	25%	75%	0%	0%	25%	100%	0%	0%				100%		
		D	8	1	13%	87%	13%	0%	0%	0%	0%	100%						100%

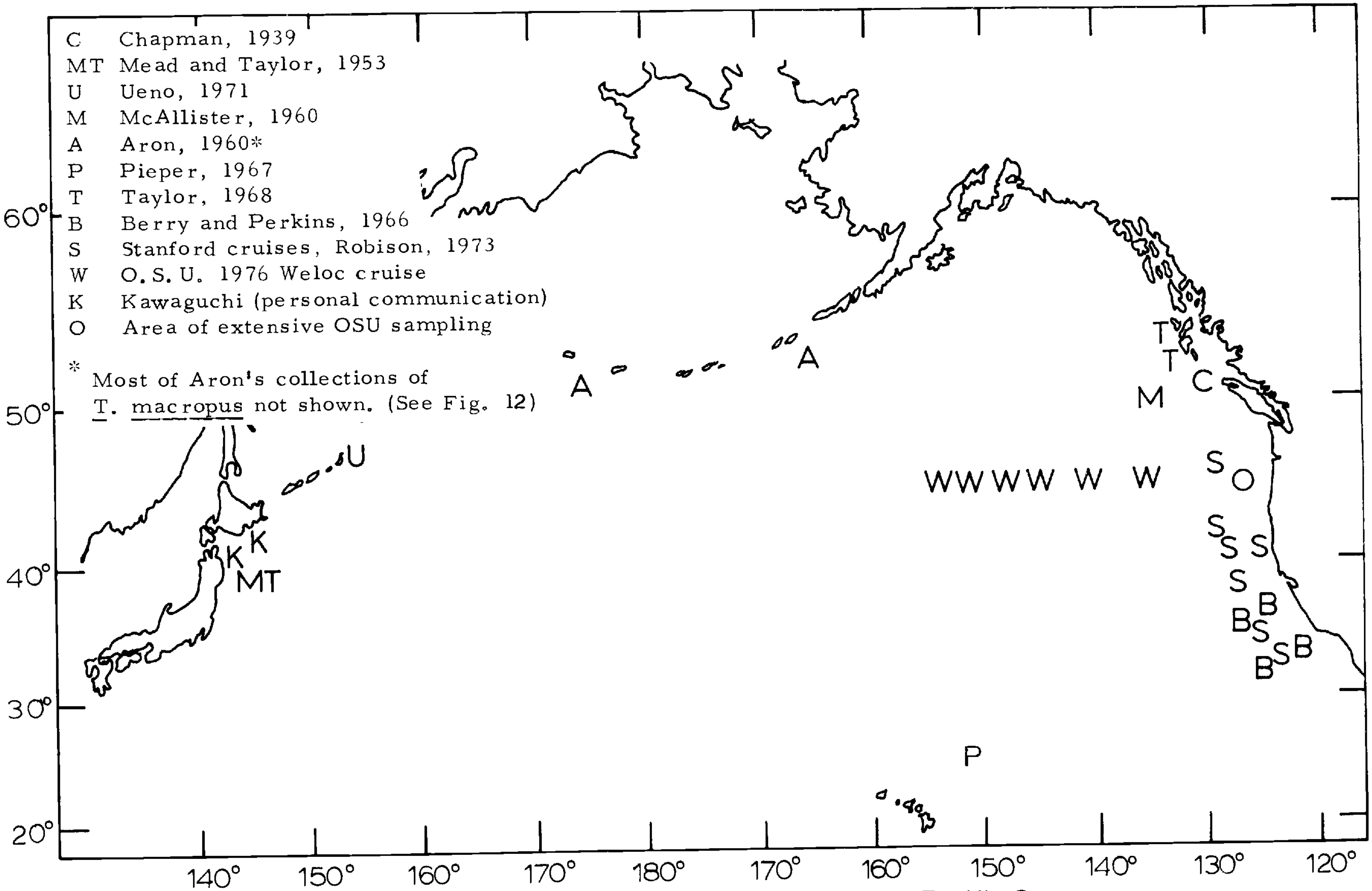


Figure 11. Collection sites of *T. macropus* in the North Pacific Ocean.

America extends from off Southern California (Berry and Perkins, 1966) to at least the Queen Charlotte Islands off British Columbia (Taylor, 1968).

Data of Aron (1960) indicate that T. macropus is abundant over a broad longitudinal range between about 42°N and 50°N latitude. He collected T. macropus during three cruises (Brown Bear 176, 199, and 202) covering an extensive area of the North Pacific. He defined 11 "areas" based upon hydrographic conditions encountered during these cruises (Table 13). His terminology on water masses and currents followed Sverdrup et al. (1942). The locations of these areas are plotted in Figure 12. Frequency of occurrence and average number of T. macropus per positive nighttime haul were calculated from his data (Table 14). Depth of hauls ranged from 20 m to 400 m with most hauls in the upper 250 meters. Data suggest that off Oregon T. macropus is abundant in this depth range at night (Pearcy et al., 1977).

The four areas with the greatest average numbers of T. macropus per positive haul were I, F, H, and K. In these four areas T. macropus occurred in from 45% to 81% of the hauls. Temperature-salinity data for these areas (Aron, 1960, 1962) indicated that the water was subarctic-transitional in character with moderate temperatures in the halocline (6°C to 10°C). High frequency of occurrence (53% and 65%) and fairly high average numbers per positive haul

TABLE 13. Hydrographic Areas Covered in Brown Bear Cruises 176, 199 and 202. Modified from Aron (1962).

Area	Cruise No.	Haul No.	Description
A	176	4-37 89-123	Offshore area not influenced by Subarctic Current
B	176	124-148	Offshore area where Subarctic Current is apparent south of 49°N latitude
C	176	38-86	The Aleutian Island Area
D	199	9-33	Area just off the Washington Coast with considerable Intermediate water present
E	199	34-95	Offshore region composed mostly of Subarctic water
F	199	96-176	Offshore region strongly influenced by the presence of Intermediate water with some Central and Equatorial water
G	199	232-284	Offshore region similar in most respects to the previous region but with greater quantities of Equatorial water
H	199	285-300	Offshore region, oceanographically intermediate between Areas E and F
I	199	301-328	Offshore region, mostly Subarctic water, but Intermediate water is present along the cruise track
J	202	16-27	Subarctic water
K	202	6-15, 33-79	Offshore region with considerable Intermediate water present

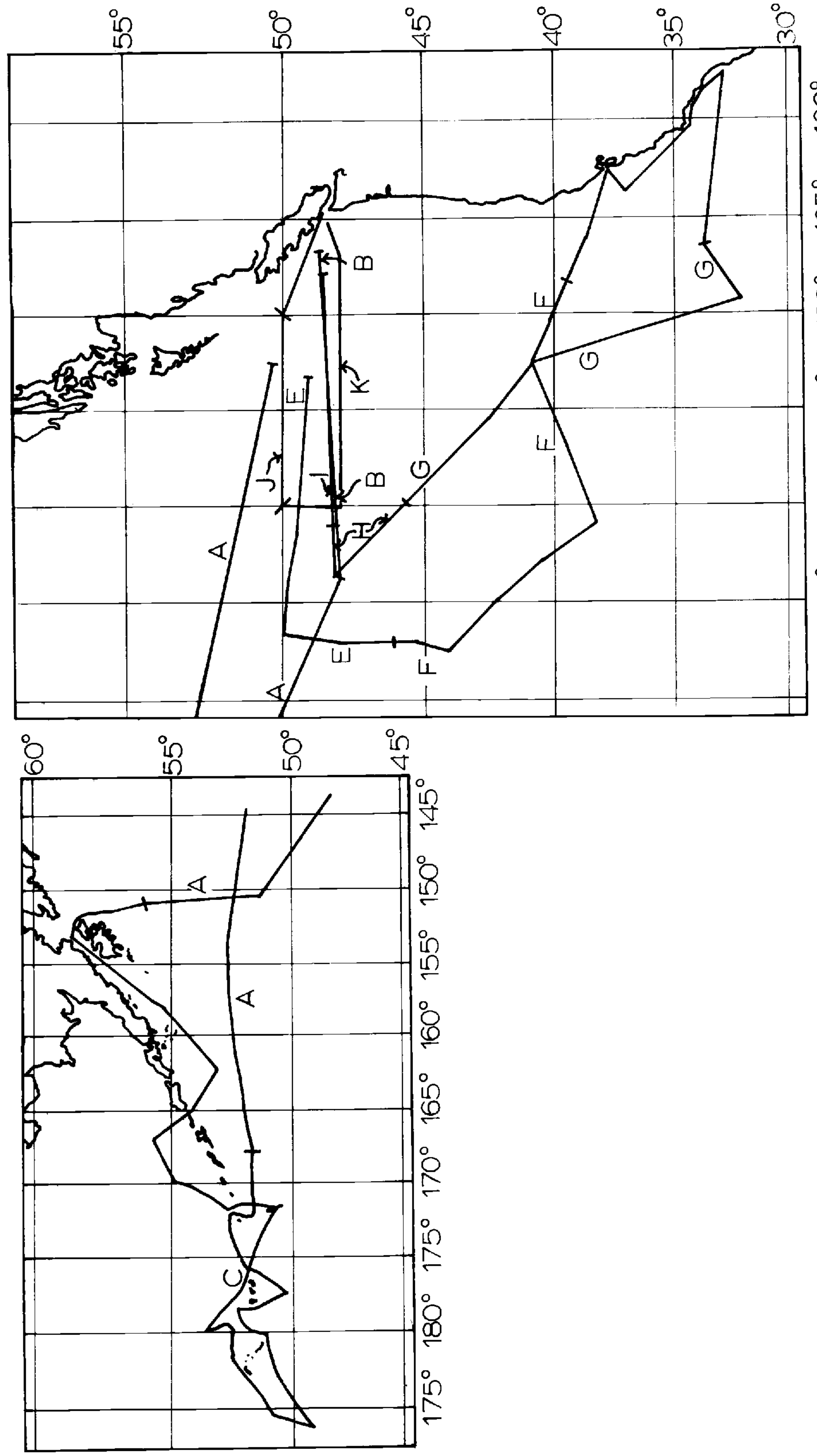


Figure 12. Cruise tracks of BB 176, 199, and 202 with Aron's hydrographic areas marked.

TABLE 14. Frequency of Occurrence and Average Number of *T. macropus* Per Positive Nighttime Haul for Each of Aron's Hydrographic Areas. Only Data From the 6' IKMT Used Except for Area I Where All Hauls Were with a 3' IKMT.

Area	No. of Hauls	No. with *T. macropus*	% with *T. macropus*	Total No. collected	Ave. no. per Haul
A	35	7	20%	8	1.1
B	23	15	65%	88	5.9
C	28	1	04%	1	1.0
D	3	0	0%	0	0
E	30	16	53%	65	4.1
F	46	24	52%	208	8.7
G	45	7	16%	9	1.3
H	16	13	81%	98	7.5
I	21	13	62%	54	4.2 (15.3)*
J	11	5	45%	13	2.6
K	47	21	45%	145	6.9

* Figure in parentheses is 3.7 x 4.2. Aron found that at 60 m depth the ratio of fish caught in the 6' IKMT to fish caught in the 3' IKMT was 3.7, all other factors being equal.

(4.1 and 5.9) also occurred in areas B and E. Area E was characterized as mostly Subarctic water with halocline temperatures of less than 6.0°C. The lowest frequency of occurrence and average number per positive haul occurred in areas A, C, and G. (Area D was not considered because of low sample size.) Area A was in the Gulf of Alaska above 50°N. Water temperatures in this area were low (around 5.0°C at 100 m). Area C was in the Aleutian Islands and had low temperatures. Area G was strongly influenced by Equatorial water and had higher temperatures.

T. macropus was among the four most abundant mesopelagic fish and was the most abundant stomiatoid collected in 0-200 m night-time IKMT hauls in the region over the outer continental slope off central Oregon (Pearcy, 1964; Pearcy and Laurs, 1966; Pearcy et al., 1977). The temperature-salinity structure of the water in this area is characteristic of modified subarctic water. Temperatures at the bottom of the permanent halocline were generally between 6°C and 8°C (Pearcy et al., 1977).

T. macropus has been collected in the western Pacific although it does not appear to be as abundant as it is off North America. Mead and Taylor (1953) collected two specimens off Northeastern Honshu, Japan in the region of mixing of the Oyashio and Kuroshio Currents. Uneo (1971) included *T. macropus* in the fauna found off the Northern Kurile Islands. K. Kawaguchi (personal communication) collected two large specimens; one off northeastern Honshu and the other off southeastern Hokkaido. Aron (1960, 1962) collected two specimens in the vicinity of the Aleutian Islands. W. G. Pearcy (personal communication) found only a few T. macropus in collections of mesopelagic fishes from the western Pacific and Bering Sea.

These data indicate that the distribution of T. macropus is associated with the Subarctic Region: the area north of a line which extends from about 40°N latitude off Japan in the region of mixing of the Kuroshio and Oyashio Currents, to about 45°N latitude at mid-ocean and then drops southward along the coast of North America. There is only one report of T. macropus from the Central water mass (Pieper, 1967).

The Subarctic region is characterized by an excess of precipitation over evaporation producing a permanent halocline in the upper waters (Uda, 1963; Dodimead et al., 1963). Across the ocean between roughly 40°N to 50°N there is a general eastward flow of water termed the "West Wind Drift" consisting of deflected water from the Oyashio Current and water formed through mixing of Kuroshio and Oyashio water (Uda, 1963; Dodimead et al., 1963). Uda (1963) found that the speed of this eastward flow is relatively uniform to about 300 m. Dodimead et al. (1963) found that in the area of the West Wind Drift the movement of the 500 decibar level relative to the 1000 decibar level is also generally eastward. As the

West Wind Drift approaches the West Coast of North America it splits at the surface at around 45°N latitude, forming the California and Alaska Currents. The Alask Current flows counterclockwise around the Gulf of Alaska, while the California Current flows south along the West Coast of North America. Dodimead et al. (1963) found that at the 500 decibar level the division of flow off the West Coast of North America was generally further south than at shallower levels. He also found that along the west coast below the permanent halocline there was generally a northward flow of water which he termed the California Undercurrent indicated by temperatures greater than 6.0°C on the 34.0‰ surface of salinity. The 34.0 salinity surface is below the permanent halocline and is effectively cut off from surface heating or cooling so any warming at this depth is most likely due to advection. Off Oregon (at around 125°W) the depth of the 34.0‰ salinity surface ranged from 200 to 400 meters between 1955 and 1959 (Dodimead et al., 1963). Between 1955 and 1959 the presence of the California Undercurrent was indicated off Oregon in 1955, 1957, and 1959 (Dodimead et al., 1963). In most of these years the Undercurrent zone off Central Oregon extended to about 127° or 128°W longitude (Dodimead et al., 1963).

The presence of the California Undercurrent off the West Coast of North America and the more southerly splitting of the West Wind Drift into north and south flowing components at depth would provide a mechanism by which mesopelagic organisms, such as *Tactostoma macropus*, which spend at least part of the day at depth, would be transported northward and perhaps be prevented from being flushed out of the Subarctic Region by the California Current.

Data presented earlier suggest that large *T. macropus* are found in greater relative abundance day and night at depths of 500 m or deeper than at shallower depths, suggesting that they do not migrate into the near surface waters at night. There is also evidence that some smaller *T. macropus* do not migrate into the near surface waters: in September 1978 27% of the *T. macropus* collected at 500 m or below at night were less than 120 mm in length. There is also good evidence that a substantial portion of the *Stenobrachius leucopsarus* population off Oregon remains at depth during the night (Pearcy et al., 1977). Large *T. macropus* and *S. leucopsarus* are probably at depth most of the time and would be transported northward in the presence of deep northward flow. The net movement of the fish would depend on the relative amounts of time they spent at depth and in the near surface waters, the speeds and directions of the currents in each zone and the speed and direction of any active migration.

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