

AN ABSTRACT OF THE THESIS OF

David Leslie Stein for the degree of Doctor of Philosophy

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Title: Aspects of Reproduction, Early Life History, and Biology of

Bathyal and Abyssal Liparididae and Macrouridae (Pisces) off Oregon.

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Carl E. Bond

The reproduction and associated biology of benthic fishes living below 2000 m is poorly known. This thesis describes the reproduction, early life history, and aspects of the natural history of macrourids and liparidids occurring on the continental slope and abyssal plain off Oregon, USA, and discusses the significance of the characteristics and differences of reproductive mode which exist in abyssal benthic fishes.

Reproduction of thirteen species of bathyal and abyssal liparidids was studied (Osteodiscus cascadiae, Acantholiparis opercularis, Paraliparis latifrons, P. rosaceus, P. megalopus, P. mento, P. cephalus, Careproctus melanurus, C. microstomus, C. oregonensis, C. ovigerum, C. longifilis, and C. filamentosus). Information on fecundity, reproductive periodicity, size at maturity and length-weight relationships was obtained from all but P. cephalus and C. filamentosus. These species can be divided into three groups based on whether they appear to spawn throughout the year or periodically. Characterization as continuous or periodic spawners was based upon presence of ripe eggs throughout the

year, presence of ripe eggs seasonally, or size distributions of ovarian eggs in ripe females. Species spawning throughout the year are primarily abyssal ( $\geq 2,100$  m). Periodic spawners are bathyal and abyssal. All ripe females had large (2.5-8.0 mm diameter) eggs. Maximum fecundities ranged from six to 1,277. Using previously published information and the new data, a possible life history for abyssal liparidids is constructed.

Few larvae of North Pacific macrourids have been identified and described. Descriptions of prejuvenile Coryphaenoides acrolepis, C. filifer, and C. leptolepis are given, with a provisional key to identification of most species occurring off Oregon. Vertical distribution of the larvae and juveniles of C. acrolepis apparently changes with ontogenetic development, the smallest individuals occurring shallowest.

Egg sizes, fecundities, times of spawning, early benthic life, size frequency, and distribution by size and sex of the four most common macrourid species occurring off Oregon (Coryphaenoides acrolepis, C. armatus, C. filifer, C. leptolepis) were studied. Egg sizes of different species at comparable stages of maturity were different. Ripe eggs were from about .60 mm to 2.1 mm diameter. Average fecundities ranged from 26,000 to 2,500,000 eggs. Two species, C. acrolepis and C. filifer, apparently spawn semi-annually; ripe females of C. armatus and C. leptolepis were not collected. Juveniles of the three sympatric species, (C. armatus, C. filifer, C. leptolepis) become benthic in habit at different sizes; C. filifer is largest. Different mouth sizes may minimize competition for food. Size frequency distributions were either unimodal (C. filifer, C. armatus) or bimodal (C. acrolepis, C. leptolepis). Small C. filifer may remain pelagic longer than other species. Coryphaenoides acrolepis and C. leptolepis were "bigger-deeper," but this trend was not evident in the other two species. Male C. armatus and C. leptolepis were less abundant than females, but males and females were equally abundant in C. acrolepis and C. filifer. There was little evidence for sexual aggregation.

Benthic fishes living below 2000 m form a group of different phylogenetic composition than deep-sea pelagic fishes. The benthic

fishes may be divided into "ancient" and "secondarily" deep-water groups, based on the kinds of adaptations present, distributions, and evolutionary history. They may also be divided into a group with high relative fecundity and small eggs, which is composed almost exclusively of ancient deep-water fishes (phylogenetically "lower" and "middle"), and a group with low relative fecundity and large eggs, which is primarily composed of secondarily deep-water fishes (phylogenetically "middle" and "advanced"). The reproductive adaptations of the second group, maximizing offspring survival, apparently allowed the radiation of some shallow-water fishes into deep water.

Aspects of Reproduction, Early Life History, and Biology of Bathyal  
and Abyssal Liparididae and Macrouridae (Pisces) off Oregon.

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Typed by Joan A. Neuman for David Leslie Stein

To William G. Percy,  
for many years of support, help, and patience

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Aspects of Reproduction, Early Life History, and Biology of Bathyal  
and Abyssal Liparididae and Macrouridae (Pisces) off Oregon.

INTRODUCTION

The deep-sea has always been a source of mystery to those associated with it. Biologists, especially, have been fascinated by its perpetual darkness and cold, sparse, strange life forms, and by the apparent stability of its physical and biological environments. Great ocean depths have stimulated research and thought since Edward Forbes (1815-1854) suggested that life did not exist below 550 m.

The bathyal and abyssal northeast Pacific Ocean was not well studied previous to the 1960's. The U.S. Fish Commission Steamer "Albatross" made a few deep-water bottom trawls off the coasts of Alaska, Washington, and Oregon in the late 19th century, but until 1962, no further work was done. Since then, members of the School of Oceanography at Oregon State University, using beam trawls and otter trawls, have extensively sampled the benthic fishes of the lower continental slope and abyssal plains off Oregon and Washington. These studies were primarily supported by the Atomic Energy Commission (now the Energy Research and Development Agency) to investigate environmental pathways of radionuclides in the deep-sea. The samples obtained have lent themselves to many other studies, and have proven to be a fertile source of new data on the systematics, taxonomy, ecology, and natural history of the fishes collected.

The studies described here have included two goals: first, to investigate how the life histories of closely and distantly related fishes are adapted to the deep-sea benthic environment; secondly, to study why the observed differences might exist, and how they have affected the composition of the benthic fish fauna. The first topic was investigated by studying the fecundities, egg sizes, early life histories, and certain other aspects of the biology of the fishes concerned. The second topic was investigated by analyzing the relationships of fecundity and egg size in deep-sea fishes to their phylogenetic histories and relationships.

A number of different factors have determined the nature of these studies. First, availability of specimens often limited the extent and interpretation of results. Additional material is difficult to acquire because of the expense and uncertainty of capture. Secondly, the sampling programs were not originally designed for the purpose of studying life histories of fishes, but rather invertebrate ecology. Furthermore, interruptions by bad weather and problems with sampling gear often resulted in lack of samples at critical times of the year or critical depths. Thirdly, fresh material was not available when the analyses were done, precluding investigation of such topics as densities of ripe eggs or buoyancy of fishes. Fourthly, one important and interesting characteristic, disproportionate liver weights in large Coryphaenoides armatus (Macrouridae) was not discovered until late in the study.

The fishes studied here are from two families not closely related: the Liparididae, a scorpaeniform family closely allied to the cottids, and the Macrouridae, a gadiform family related to the cods. The liparidids are the most speciose fish family occurring below 1000 m off Oregon; the macrourids are the fish family most abundant by numbers and by weight. In general, adult macrourids are much larger than adult liparids. Although members of both families are often captured in the same tows as adults, they probably have slightly different distributions. Many liparidids probably rest directly on the bottom; macrourids swim just above it, often hanging motionless in the water. Despite the abundance of both families at bathyal and abyssal depths, only their taxonomy is reasonably well known.

The series of papers that comprise this thesis represent most of the recorded data on reproduction, early life history, and associated biology of the Oregon fishes described above. This new information shows that the fishes living in the relatively stable and unchanging benthic deep-sea environment have widely divergent adaptations to it. These adaptations probably have had an important role in determining the phylogenetic composition of the benthic fish community.

## II. Aspects of Reproduction of Liparid Fishes from the Continental Slope and Abyssal Plain off Oregon, with Notes on Growth

DAVID L. STEIN

Reproduction of 13 species of bathyal and abyssal benthic liparids (*Osteodiscus cascadiae*, *Acantholiparis opercularis*, *Paraliparis latifrons*, *P. rosaceus*, *P. megalopus*, *P. mento*, *P. cephalus*, *Careproctus melanurus*, *C. microstomus*, *C. oregonensis*, *C. ovigerum*, *C. longifilis*, and *C. filamentosus*) off the coast of Oregon was studied. Information on fecundity, reproductive periodicity, size at maturity and length-weight relationships were obtained from all but *P. cephalus* and *C. filamentosus*. These species can be divided into three groups on the basis of fecundity relationships, and into two groups based on whether they appear to spawn throughout the year or periodically. Characterization of species as continuous or periodic spawners was based upon presence of ripe eggs throughout the year, presence of ripe eggs seasonally, or size distributions of ovarian eggs in ripe females.

Species which spawn throughout the year are all primarily abyssal (>2,100 m). Those spawning at relatively long intervals (the durations and frequencies of which are generally unknown) are bathyal and abyssal. All ripe females had large (2.5-8.0 mm diameter) eggs. Maximum fecundities of the species ranged from six to 1,277.

Based upon previously published information and the new data, a possible life history for abyssal liparids is constructed.

THE Liparidae contains several hundred species, occurs in all the oceans of the world and is distributed from the intertidal to the hadal zones. Despite this, little is known about liparid reproduction.

Knowledge about liparid reproduction is of interest and importance. First, because the family is one of the few with an extremely broad depth distribution, it allows comparison of reproductive habits of relatively closely related shallow and deep water species. Second, such knowledge can help decide whether or not deep sea animals reproduce periodically or continuously.

Most knowledge of liparid reproduction concerns shallow water species. Able and Musick (1976: *Liparis inquilinus*) and Detwyler (1963: *Liparis atlanticus*) described egg sizes, spawning periods and growth of the two species. There have been many miscellaneous observations of egg size, development or time of spawning in various species (McIntosh, 1885; Collett, 1909; Schmidt, 1916; Aoyama, 1959; Johnson, 1969; Hart, 1973; DeMartini, 1978).

Much less is known about reproduction of deep water species. Since the review of reproduction in deep water liparids included in Mead et al. (1964), little knowledge has been added. Cohen (1968) mentioned egg sizes of

*Paraliparis calidus*. Wenner (1979) described the occurrence of *Paraliparis garmani*, *P. copei*, *P. calidus*, sizes of ovarian eggs, testes and feeding habits, and speculated about possible mouth brooding by *P. garmani* males. Some species of *Careproctus* are known to lay eggs in lithodid crabs (Hunter, 1969; Parrish, 1972; Peden and Corbett, 1973).

This paper describes the results of a study of the eggs, fecundity, reproductive periodicity, size at maturity and length-weight relationships of 13 species of liparids in four genera. These species occur between 200 and 3,585 m off the coast of Oregon, and were described or redescribed by Stein (1978). They are *Careproctus longifilis* Garman, *C. microstomus* Stein, *C. filamentosus* Stein, *C. oregonensis* Stein, *C. ovigerum* (Gilbert), *C. melanurus* Gilbert, *Osteodiscus cascadiae* Stein, *Acantholiparis opercularis* Gilbert and Burke, *Paraliparis rosaceus* Gilbert, *P. megalopus* Stein, *P. cephalus* Gilbert, *P. latifrons* Garman, and *P. mento* Gilbert.

### MATERIALS AND METHODS

All but 11 of the specimens examined were obtained from the bottom trawl collections described by Stein (1978) and made over a period of about 14 years. Eleven specimens of *C. me-*

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TABLE 1. SPECIES EXAMINED, THE DEPTHS FROM WHICH THEY CAME, NUMBERS EXAMINED AND THE MONTHS IN WHICH THEY WERE COLLECTED. Months were not sampled equally. Numbers of specimens do not represent relative abundances of individuals within or among species.

Species	Depth (m)	N	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
<i>A. opercularis</i>	1,900-2,997	61		10	35			3	7	2	2			2
<i>C. filamentosus</i>	2,850	1		1										
<i>C. longifiliis</i>	2,803-2,816	3		1	1									1
<i>C. melanurus</i>	190-1,600	26	2		3	3		8	4	1	2	2	1	
<i>C. microstomus</i>	2,740-3,585	3		1	1							1		
<i>C. oregonensis</i>	1,900-2,760	2					1		1					
<i>C. ovigerum</i>	2,510	1									1			
<i>O. cascudiae</i>	1,900-2,997	130	6	28	26		6	14	17	6		12	15	
<i>P. cephalus</i>	580-960	12	1		3	1		2	4	1				
<i>P. latifrons</i>	2,225-2,763	38			14				8		14	2		
<i>P. megalopus</i>	2,825-3,585	5	1					1		1		2		
<i>P. mento</i>	800-960	2	2											
<i>P. rosaceus</i>	2,540-2,809	5	1		4									

*lanurus* were borrowed from the fish collection of the Department of Fisheries and Wildlife, Oregon State University. All specimens were initially fixed in 10% formalin solution and later transferred to 45% isopropanol. Standard lengths of all individuals were measured to the nearest millimeter. Specimens were weighed to the nearest 0.1 g. When possible, both ovaries of females were removed, lightly blotted with absorbent paper, and weighed to the nearest 0.001 g. Such accuracy was necessary because ovaries and testes of immature individuals often weighed less than 0.001 g. Both testes of male *Acantholiparis opercularis*, *Paraliparis latifrons* and testes of selected males of other species were removed, blotted and weighed as above.

Eggs were measured to the nearest 0.17 mm using an ocular micrometer and a binocular dissecting microscope. All measurements are of greatest diameter of preserved eggs. Johnsen (1921) found that 5.0-5.5 mm fresh eggs could shrink 0.3-1.0 mm in preservation. Because all specimens were preserved similarly, it was assumed that egg sizes, ovary weights, standard lengths and fish weights were comparable. When <50 ripe eggs/ovary were present, all eggs (from both ovaries) with a largest diameter greater than or equal to 0.37 mm (the size below which egg measurement and enumeration was too difficult) were measured and counted. With the exception of the eggs of *C. ovigerum*, if >50 ripe eggs/ovary were present a representative subsample (ca. 50 ripe eggs plus a proportionate number of unripe eggs) was removed after ascertaining the intra-ovarian

distribution of eggs of different sizes. The subsample was weighed and the eggs in it measured and counted. The number of eggs of different sizes contained in the whole ovary and both ovaries were then estimated by proportion. In *C. ovigerum*, because of the size of the ovaries and difficulties involved in adequately subsampling the eggs, only eggs from the right ovary >2.87 mm were counted and measured. Fecundity was estimated as the total number of ripe eggs present in each female.

Mature (ripe) eggs were comparatively very large, yolk-filled, barely translucent, with a hard, tough chorionic membrane, almost completely free of ovarian tissues within the ovary (i.e. nearly ovulated). Maturing (ripening) eggs were large, yolky, with a tough chorionic membrane, firmly held in ovarian tissue. Immature eggs were relatively small, transparent, yolk-free, very firmly embedded in ovarian tissues.

Females considered ready to spawn or spawning (ripe) had ovaries containing mature eggs. Spawning females had ovaries with ripe eggs and "large empty spaces" (usually clearly the size and shape of individual ripe eggs). Spent females had flaccid ovaries with no ripe eggs present. All females longer than the shortest female of that species having ripe eggs were considered mature, whereas all females shorter than the shortest female with ripe eggs were considered immature. Minimum length at female maturity was that of the shortest female with ripe eggs of that species.

Ripe males had swollen, translucent, white, reticulated testes. Unripe males had thin,

## STEIN—LIPARID REPRODUCTION

opaque, cream-colored, usually short testes. Minimum length at male maturity was that of the shortest male with ripe testes of that species.

Conclusions concerning continuity of spawning were based on times of occurrence of ripe females and on size distributions of ovarian eggs in ripe females. Species were considered to be "continuous" spawners if ripe females were captured throughout the year or if ovarian egg sizes in ripe females were widely distributed ("long spawning period" of Hickling and Rutenberg, 1936). Species were considered to be "periodic" spawners if ripe females were present part of the year or if size distributions of ovarian eggs in ripe females were narrowly distributed ("short and definite spawning period" of Hickling and Rutenberg, 1936).

Length-weight relationships were described using a regression equation of the general form  $W = aSL^b$ , where  $W$  = whole body weight in grams,  $SL$  = standard length in mm, and  $a$  and  $b$  are constants.

## RESULTS

*Osteodiscus cascadiae*: One hundred thirty individuals (69 females, 30–81 mm; 61 males, 33–71 mm) captured during nine months of the year (Table 1) were examined. All males with large testes had a prominent genital papilla.

Maximum egg diameter was 5.29 mm. Eggs were not segregated by size within the ovaries; the largest eggs occupied most of the space, with smaller eggs filling the interstices. Those  $>2.00$  mm occurred in distinct size groups composed of few eggs (Fig. 1). Three females had eggs  $>5.00$  mm, 18 females had eggs between 4.00 and 4.99 mm and 9 had eggs between 3.00 and 3.99 mm. The total number of ripe eggs ( $>4.00$  mm)/female ranged from 1 to 7, the mean was 4.05 and the mode was 3 (6 females). There was no clear relationship between fecundity and length. Females mature by ca. 65 mm (Fig. 2).

Ripe females occurred in January, February, March, May, June, July and October. Females which appeared to have spawned recently occurred in March, June and July (Fig. 3). Adult females with maturing eggs, ready to spawn or spent occurred simultaneously (Fig. 1). Ripe males were found in February, March, May, June, July and October. Spawning probably takes place all year, eggs being laid in small clutches or (perhaps) singly.

Length-weight relationships of females and

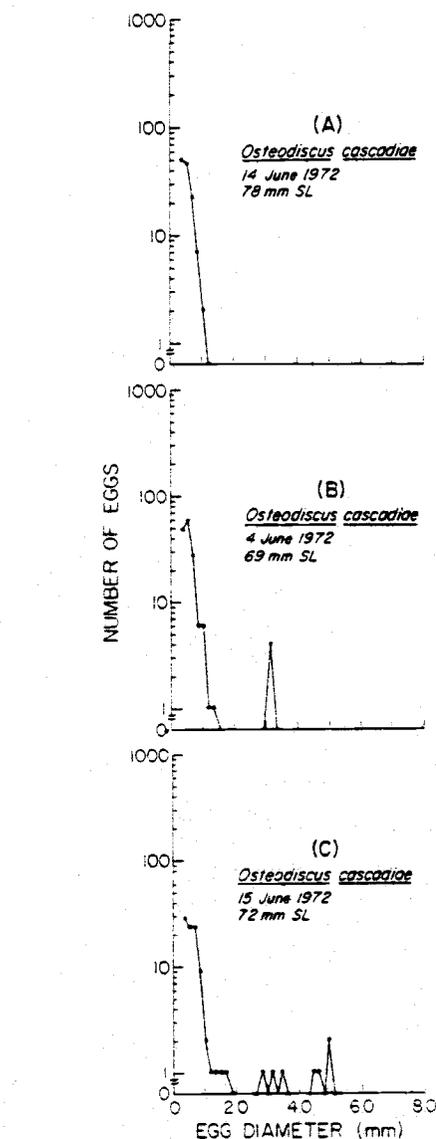


Fig. 1. Size distributions of ovarian eggs in three mature females (A) spent, (B) with maturing eggs, (C) ready to spawn) of *Osteodiscus cascadiae* captured within two weeks.

males are described by  $W = 3.303 \times 10^{-6}SL^{3.13}$ , and  $W = 1.294 \times 10^{-5}SL^{2.70}$  respectively. Length-weight relationships for all individuals are described by  $W = 5.268SL^{3.00}$ . Large variations in adult female weights result from the highly variable number of large eggs present.

*Acantholiparis opercularis*: Sixty-one individuals (36 females, 34–75 mm; 25 males, 32–58 mm) were examined. They were captured during

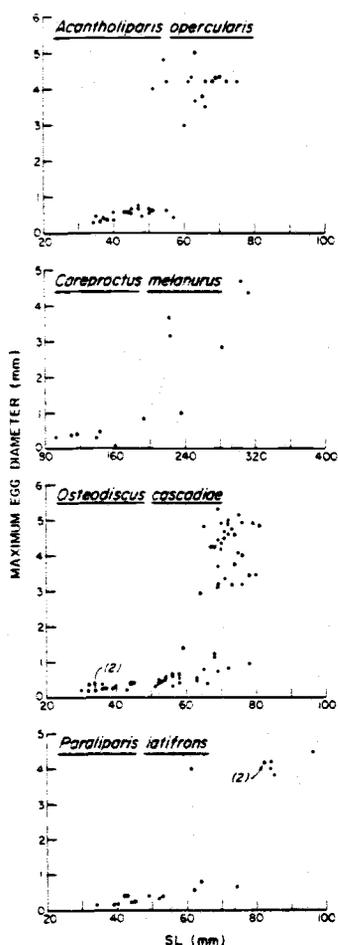


Fig. 2. Standard lengths at sexual maturity of female *Acantholiparis opercularis*, *Careproctus melanurus*, *Osteodiscus cascadae* and *Paraliparis latifrons*.

seven months of the year (Table 1). No distinct external sexual dimorphism was evident.

Maximum egg diameter was 4.96 mm, but the one egg of this size may have been distorted; the next largest egg was 4.80 mm. Egg distribution in the ovaries was similar to that in *O. cascadae*. Eggs occurred in distinct size groups, each of which contained relatively few eggs except for those less than 1.00 mm (Fig. 4). Twelve females, SL 51–75 mm, had ripe eggs (>4.00 mm). No female less than 51 mm had eggs >0.74 mm. The number of ripe eggs per female ranged from 1 to 6; the mean number of ripe eggs was 3.2, although the mode was 1. Only females 65 mm or longer contained 4 or more ripe eggs. One 51 mm female had a ripe egg in the right ovary and none over 0.50 mm in the left.

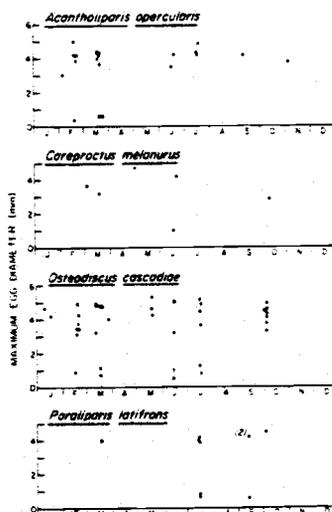


Fig. 3. Maximum size of ovarian eggs present in mature individuals of *Acantholiparis opercularis*, *Careproctus melanurus*, *Osteodiscus cascadae* and *Paraliparis latifrons* at date of capture. ○ = spent or spawning individual.

Females mature by ca. 51 mm SL (Fig. 2). Length of males at maturity could not be determined from the specimens available.

Ripe females occurred in February, March, June, July, September and possibly November. Possibly spent females occurred in February and March (Fig. 3). Males which appeared ripe occurred in March, July and August. Spawning probably takes place throughout the year, few eggs being laid at any one time.

Length-weight relationships of females and males are about the same,  $W = 8.136 \times 10^{-7}SL^{3.46}$  and  $W = 9.423 \times 10^{-7}SL^{3.41}$ , respectively. The combined relationship is  $W = 8.05 \times 10^{-7}SL^{3.45}$ .

*Paraliparis latifrons*: Thirty-eight specimens (22 females, 34–96 mm; 16 males, 31–88 mm), captured during four months of the year (Table 1), were examined. Males with ripe testes had a well developed genital papilla.

Maximum egg diameter was 4.47 mm. Egg distribution within the ovaries was similar to that of *O. cascadae*. Eggs formed distinct size groups; groups of eggs >1.35 mm contained relatively few eggs (Fig. 4). Six females, 61–96 mm, had 2 to 8 ripe eggs (>4.00 mm); the mean was 3.7, the mode was 2. Although the 96 mm female had the most ripe eggs, there was no clear relationship between length and number

## STEIN—LIPARID REPRODUCTION

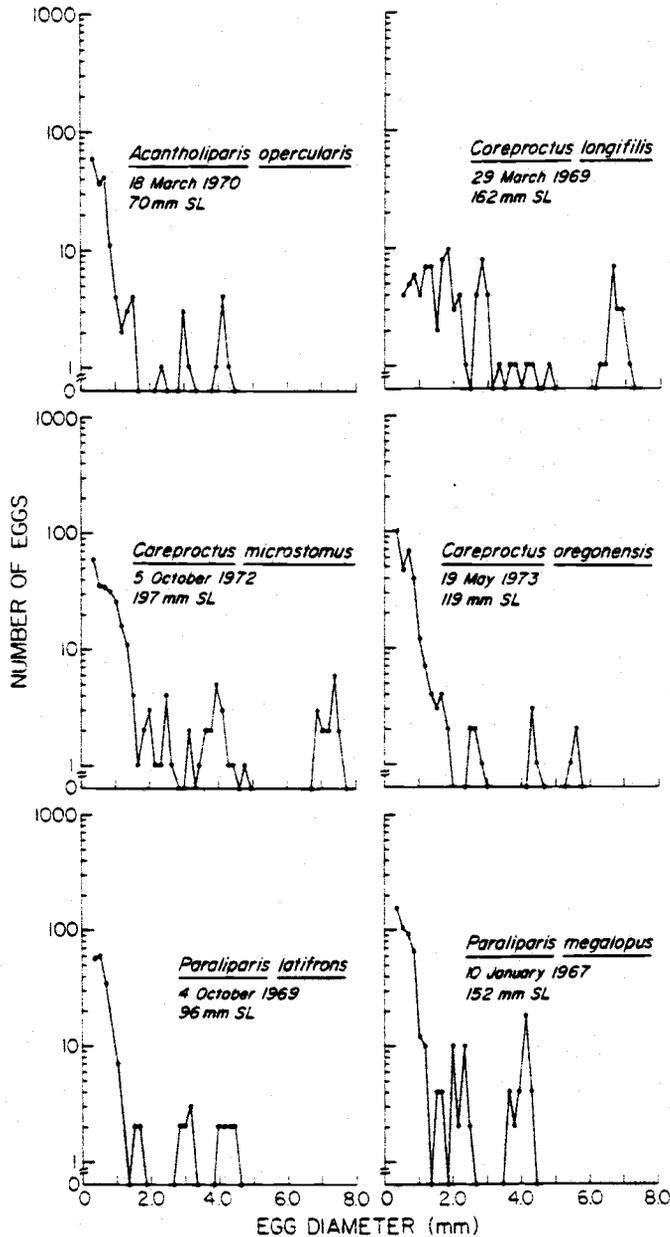


Fig. 4. Size distributions of ovarian eggs in individual mature females of *Acantholiparis opercularis*, *Careproctus longifilis*, *C. microstomus*, *C. oregonensis*, *Paraliparis latifrons* and *P. megalopus*, with dates of captures and SL.

of ripe eggs. Females mature at about 61 mm (Fig. 2).

Ripe females were captured in March, July, September and October (Fig. 3). Apparently ripe males were collected in March and September. Spawning in this species probably occurs throughout the year.

The length-weight relationship for both

sexes combined is described by  $W = 6.56 \times 10^{-7}SL^{3.47}$ . The length-weight relationship of females is described by  $W = 5.19 \times 10^{-6}SL^{2.99}$ . Insufficient numbers of males were examined to determine a separate L/W curve.

*Careproctus melanurus*: Twenty-six specimens (15 females, 92–312 mm; 11 males, 126–278

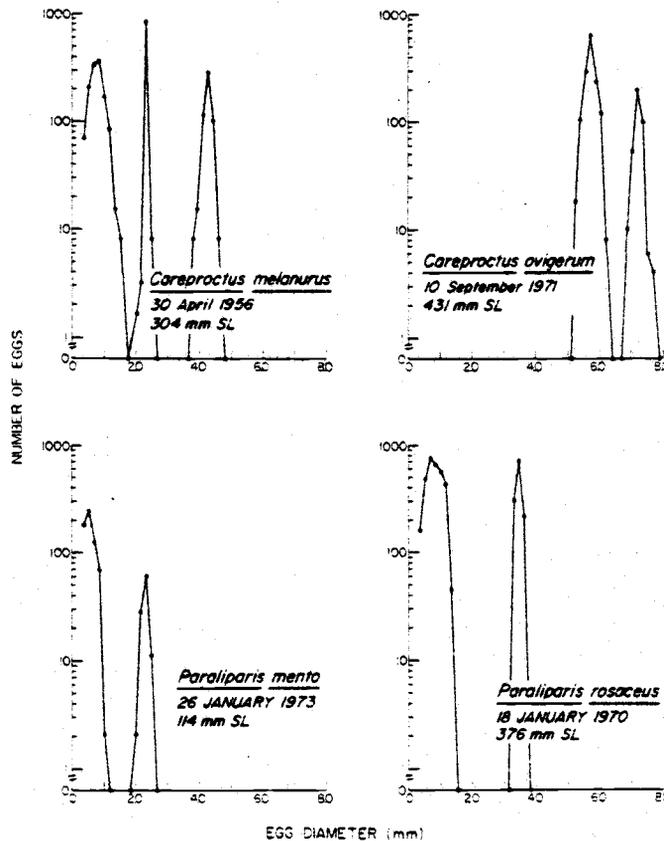


Fig. 5. Size distributions of ovarian eggs in individual mature females of *Careproctus melanurus*, *C. ovigerum*, *Paraliparis mento* and *P. rosaceus*, with dates of capture and SL. Eggs of *C. ovigerum* smaller than 2.87 mm were not counted.

mm) captured during nine months of the year (Table 1) were examined. Mature males are externally distinguishable from females by possession of a genital papilla up to 7 mm long.

Maximum egg diameter was 4.63 mm; these eggs were completely free within the lumen of the ovary. Ripe eggs (>3.84 mm) filled the anterior half of the ovary and distinctly smaller unripe eggs filled the posterior half. Maximum observed fecundity was 534. Ripe eggs composed up to 73% of ovarian weight. The ripe eggs form a group widely separated from the smaller eggs (Fig. 5).

Length of female *C. melanurus* at maturity could not be precisely determined because of small sample size and highly variable egg size, but it appears to be between 200 and 220 mm (Fig. 2). Sample size was too small to conclude that the sexes have different maximum sizes.

Spawning may be seasonal; the only females with eggs over 4.0 mm were captured in April

and June (Fig. 3) although large females were collected in March, April, June and October. Males with the largest testes were collected in June (0.85% total weight) and in September (0.93% total weight). Ripe or maturing females were collected at 200, 265, 274–430 and 1,300 m depth.

The length-weight relationship for both sexes combined is described by  $W = 8.160 \times 10^{-6}SL^{3.09}$ ; for females, by  $W = 7.617 \times 10^{-6}SL^{3.10}$ . Insufficient numbers of males were examined to determine a separate L/W curve.

*Careproctus microstomus*: Three females (178, 183, 197 mm) captured in February, March and October, respectively, were examined.

Maximum egg diameters were 6.60 mm, 6.11 mm and 7.58 mm, respectively. The ovaries of the longest female contained 15 ripe eggs ( $\geq 7.00$  mm); the next largest eggs present were 4.76 mm (Fig. 4). Ovaries of the other females

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contained no eggs as large as 7 mm but did have 11 (left ovary only) and 19 (both ovaries) eggs >6.00 mm. The largest eggs of the 178 mm female each contained a distinct, large oil droplet.

Size distributions of ovarian eggs of three ripe females suggest that members of this species may spawn continuously.

*Paraliparis rosaceus*: Five females (288–361 mm) captured in January and March, were examined.

The largest egg was 3.65 mm. A number of distinct size groups were present in two specimens. The ovaries of a female (ca. 350 mm) ready to spawn captured in January were swollen and contained two groups of eggs: 3.32–3.65 mm, and <1.35 mm (Fig. 5). Estimated number of ripe eggs was 1,277. The ovaries of another female (333 mm SL) captured in March, did not contain any eggs larger than 1.68 mm.

*P. rosaceus* appears to spawn at least in the winter. The 333 mm female discussed above could have spawned earlier. A third female (March; 361 mm) had a group of relatively small developing eggs, perhaps indicating recovery from a much earlier spawning.

*Careproctus oregonensis*: Two females (119, 153 mm) captured in May and July, were examined. Largest eggs were 5.62 mm and 5.29 mm respectively. The ovary of the larger female contained five eggs  $\geq$ 5.00 mm and five eggs between 4.51–4.99 mm. The ovary of the smaller contained three eggs  $\geq$ 5 mm and four eggs between 4.26 mm and 5.00 mm diameter (Fig. 4). Size distributions of ovarian eggs of the ripe females suggest that this species may have prolonged or continuous spawning.

*Careproctus ovigerum*: One female, 431 mm, captured in September, was examined. Maximum egg diameter was 7.75 mm. The right ovary contained 936 eggs >5.25 mm, grouped in two distinct size modes close together but widely separated from the next largest eggs (2.87 mm) (Fig. 5). Estimated number of ripe eggs (6.93–7.75 mm) in both ovaries of the specimen was 756. These eggs were free in the lumen of the ovary; immature eggs were peripheral to them. Size distribution of ovarian eggs in this female suggests spawning periods separated by long intervals.

*Paraliparis megalopus*: Five specimens (three females, 137, 150, 152 mm; two males, 114, 132 mm) captured during four months of the year (Table 1), were examined.

There was no obvious sexual dimorphism. Only one female (152 mm, collected in January) had large eggs, of which the largest was 4.31 mm. Egg size groups were not quite as distinct as those of many of the other species studied, although the pattern was similar to those of the continuous spawners (Fig. 4). There were 32 ripe (>3.62 mm) eggs present with many groups of smaller eggs also present. The males, captured during October, were apparently ripe. Size distribution of ovarian eggs in this female possibly suggest prolonged or continuous spawning.

*Careproctus longifilis*: Three female specimens, 146, 162, 162 mm, captured in February, March and November, respectively, were examined. The female collected in November had eggs up to 7.09 mm diameter (Fig. 4). There were 16 ripe (>6.31 mm) eggs present. The 146 mm specimen contained eggs up to 1.52 mm; the 162 mm female collected in March had only eggs <0.86 mm. Size distribution of ovarian eggs in a ripe female possibly suggests prolonged or continuous spawning.

*Paraliparis mento*: Two specimens (female, 114 mm; male, 95 mm), captured in January (Table 1), were examined. There was no obvious sexual dimorphism. The largest egg was 2.50 mm. Eggs of different sizes were evenly distributed throughout the ovaries. There were two groups of different size eggs: (ripe) 2.00–2.50 mm (101 eggs) and <1.00 mm (Fig. 5). The male appeared to be ripe. Size distribution of ovarian eggs in the ripe female suggests possible periodic spawning.

*Paraliparis cephalus*: Twelve specimens (six females, 37–83 mm; six males, 58–82 mm) captured during six months of the year (Table 1) were examined. There was no obvious sexual dimorphism. Maximum egg diameter was 0.86 mm. No females had mature eggs. One male (82 mm) captured in January had well developed testes and seemed to be ready to spawn. No conclusions were made about reproduction of this species.

*Careproctus filamentosus*: One female (180 mm) captured in February was examined. The larg-

est eggs were 0.70 mm; they were obviously immature, with no obvious yolk, and a thin outer membrane. The ovaries were relatively small. There were no signs of recent spawning. No conclusions were made about reproduction of this species.

#### DISCUSSION

The question of whether seasonal reproduction exists at abyssal depths has been discussed at least since Orton (1920) proposed that animals living in stenothermal environments (polar seas, great depths, tropics) reproduce continuously. Although the evidence is not abundant, recent studies have shown that at least some endemic Antarctic benthic fishes have distinctly seasonal reproduction (Hureau, 1970) and that tropical reef fishes may either have spawning peaks (Munro et al., 1973) or prolonged but distinct seasonal reproductive periods (Russell et al., 1977). Until now there has been little evidence for or against the existence of seasonal spawning of fishes in the abyss.

Menzies et al. (1973) reviewed the evidence for seasonal and continuous spawning of abyssal fishes and invertebrates. Based on their own studies of isopods and on those of other groups by other authors, Menzies et al. concluded that "the fauna . . . tends to show definite reproductive periodism" but were unable to demonstrate an environmental cue for it. Rokop (1974) found year round asynchronous reproduction in bathyal brittle stars and crustaceans, continuous reproduction in bivalves and a polychaete, and seasonal reproduction in a bathyal brachiopod and scaphopod. The last two were species from the continental shelf whose distributions extended into bathyal depths. He concluded that "year-round reproduction is the common pattern in the deep-sea benthos."

There is substantial evidence to show that bathyal fish species (primarily macrourids) exhibit either seasonal or continuous reproduction. Novikov (1970), Savvatimskii (1969), Haedrich and Polloni (1976), S.I.O. (1975) and Rannou (1976) showed that a number of different macrourid species which live on the continental slope have definite seasonal spawning. Nielsen (1969) concluded that an aphyonid, also from the continental slope, has continuous spawning. Mead et al. (1964) suggested that abyssal benthic fishes would spawn continuously, perhaps show parental care, and would have low fecundity with large eggs. Rannou

(1975) proposed that at least some abyssal fishes spawn periodically, based on the presence of "growth checks" (similar to those in otoliths of shallow water fishes) in the otoliths of *Coryphaenoides guentheri* (Macrouridae, 1,800–3,000 m), *Bathysaurus mollis* (Bathysauridae, 4,240 m), *Histiobranchus bathybius* (Synphobranchidae, 4,700 m), *Antimora rostrata* (Moridae, 1,909 m), *Coryphaenoides leptolepis* (Macrouridae, 4,256 m) and *C. armatus* (Macrouridae, 4,256 and 2,750 m), and on the presence of a single group of larvae in the ovaries of *Cataetx laticeps*, a viviparous brotulid from 1,889 m. Rannou himself pointed out that he did not know the length of the periods which he felt were represented by the "checks."

The conclusions reached here are that continuous spawning, and possibly periodic spawning (deposition of eggs at relatively long intervals), exist in abyssal benthic liparids, and that at least some slope liparids probably spawn seasonally. The species examined here can be tentatively divided into two classes: continuous spawners and periodic (at least some of which are probably seasonal) spawners. Species were assigned to a group based upon capture of ripe females throughout the year (*O. cascadiae*, *P. latifrons*, *A. opercularis*), capture of ripe females during part of the year (*C. melanurus*), and egg size distributions in ripe females (all other species).

Following the logic of Hickling and Rutenberg (1936), de Vlaming (1974) and Rannou (1975), the presence of only one size group or two similar size groups of ripe (yolked) eggs, absence of intermediate size eggs, and presence of a group of immature (yolkless) eggs indicates that a species probably spawns only at relatively long intervals. Conversely, presence of many egg size groups indicate prolonged or continuous spawning. Based on these criteria, continuous spawners probably include *Careproctus longifilis*, *C. microstomus*, *C. oregonensis*, *Osteodiscus cascadiae*, *Acantholiparis opercularis*, *Paraliparis megalopus* and *P. latifrons*. The periodic group probably includes *Careproctus melanurus*, *C. ovigerum*, *Paraliparis mento* and *P. rosaceus*. Rates of oogenesis are unknown for any abyssal fishes. Rates of egg development in the above species could be very slow, individual females spawning at long intervals, but asynchronously with most conspecifics. Although it is evident that spawning is asynchronous in *O. cascadiae*, *A. opercularis* and *P. latifrons*, it seems unlikely that females spawn only at long intervals. Al-

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TABLE 2. SPECIES MAXIMUM FECUNDITY GROUPS, MAXIMUM FECUNDITY/FEMALE, MAXIMUM EGG DIAMETERS, SL, AND MAXIMUM PERCENT TOTAL BODY WEIGHT REPRESENTED BY THE OVARIES. C = continuous, P = periodic spawning.

Group	Species	Fecundity	Max. egg diam. (mm)	Max. SL	% ovary wt.	Spawning
I	<i>A. opercularis</i>	6	4.96	75	16.95	C
	<i>C. oregonensis</i>	10?	5.62	153	9.98	C
	<i>O. cascadiae</i>	7	5.29	81	8.33	C
	<i>P. latifrons</i>	8	4.47	96	9.21	C
II	<i>C. longifilis</i>	16	7.09	162	6.99	C
	<i>P. megalopus</i>	32	4.31	152	7.60	C
	<i>C. microstomus</i>	15	7.58	197	5.80	C
III	<i>P. mento</i>	101	2.50	114	10.32	P
	<i>C. melanurus</i>	534	4.63	312	4.43	P
	<i>C. ovigerum</i>	756	7.75	431	1.23	P
	<i>P. rosaceus</i>	1,277	3.65	361	6.66	P

most all adult females had ripe eggs. If spawning occurs at long intervals and egg development is slow, many adult females without ripe eggs should have been captured. Fecundity is extremely low in many species, which, if spawning occurred at long intervals, would result in few offspring. Very few spent *O. cascadiae* and *A. opercularis* and no spent *P. latifrons* were captured. Furthermore, the presence of distinct groups of ripening (intermediate size) eggs may be evidence for relatively frequent replacement of spawned eggs. It seems most likely that spawning is not only asynchronous but that females spawn relatively frequently throughout the year.

The continuous spawning group includes three species which are known to spawn throughout the year: *O. cascadiae*, *A. opercularis* and *P. latifrons*. Ripe females of the first two species were captured during all seasons, and the last during three seasons of the year. Adults of all of these species are less than 200 mm long, and have similar size distributions and numbers of eggs. They have few (often very few) ripe eggs present at one time; the largest eggs are distinctly but not necessarily widely separated from the next largest size mode of eggs; and there is usually at least one group of intermediate sized eggs between the smallest, least mature eggs and the largest, most mature ones. All the species in this group are abyssal: the shallowest occurring species are *C. longifilis* and *A. opercularis*, which reach 1,900 m, the base of the continental slope. Mature female *O. cascadiae* captured in the same month were

found with ripe eggs present in various numbers; spent, with no large eggs and no intermediate (maturing) eggs; and with maturing eggs (Fig. 1). Males of these species appear to be ripe throughout the year. *Careproctus longifilis*, *C. microstomus*, *C. oregonensis* and *P. megalopus* were included on the basis of egg size distributions and occurrence of ripe males.

Evidence is strongest for "periodic" spawning of *C. melanurus*, which possibly spawns in spring and summer. The only running ripe female found was captured at the end of April. Peden and Corbett (1973) found eggs off British Columbia in June, which they concluded (based on meristic characters of larvae and size of egg masses) were probably from *C. melanurus*. Parrish (1972) reported larvae and hatching eggs off Monterey, California in mid-October, although he did not describe how they were identified. These occurrences are widely separated geographically, and may have been from waters of different temperatures. *C. melanurus* may have a prolonged spawning season from early spring to late summer (depending on presently unknown factors).

Why *C. ovigerum* and *P. rosaceus*, the two largest (of ten) abyssal species, would have periodic reproduction is unclear. Stein (1978) suggested that *C. ovigerum*, which displays few of the morphological characteristics of "typical" abyssal liparids, represents a more recent invasion of deep water by liparids. Periodic spawning of this species could be a relict behavior. Shallow water liparids spawn seasonally, although spawning periods may be prolonged (Detwyler,

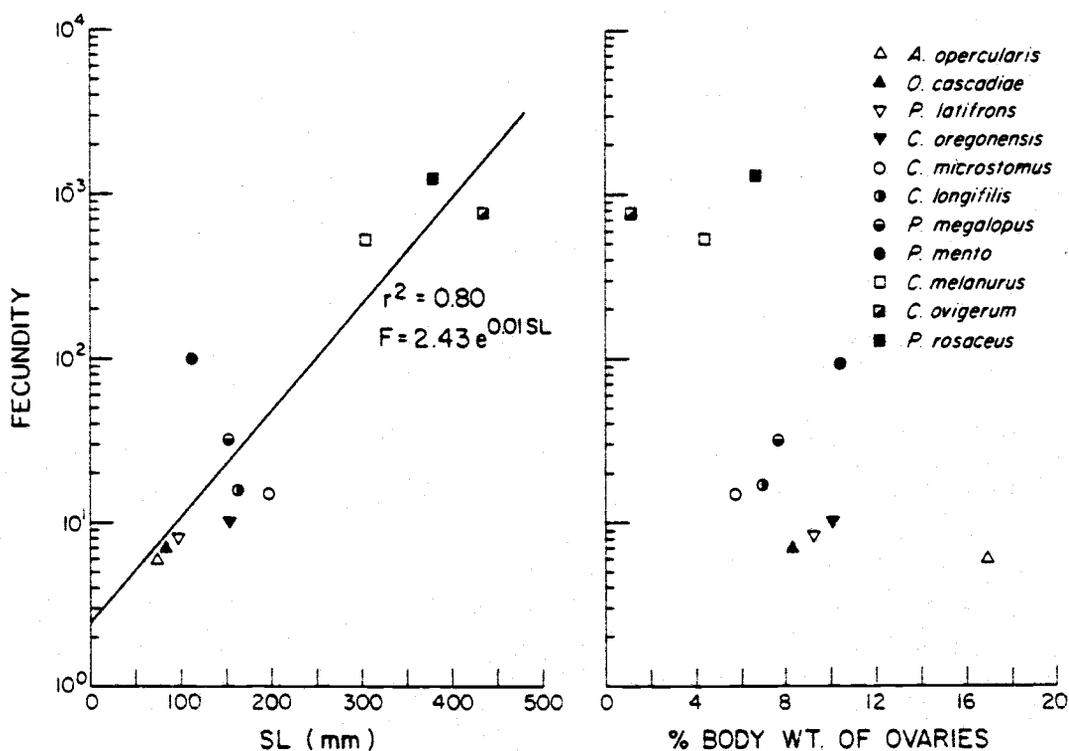


Fig. 6. Relationship of maximum fecundity vs. maximum SL and maximum % body weight of ovaries for 11 species of liparids.

1963; Breder and Rosen, 1966; Able and Muisick, 1976). However, *Paraliparis rosaceus* is a typical abyssal liparid in all respects except, perhaps, its size. It has a relatively wide depth distribution (1,799–3,358 m) (Stein, 1978), which extends up onto the lower continental slope, where it could be affected by seasonally occurring environmental events.

These liparid species can also be divided into three groups based upon maximum fecundity (Table 2). These groups are: Group I, species producing fewer than ten ripe eggs at one time; Group II, species with 10–100 ripe eggs; Group III, species producing more than 100 ripe eggs at once. These groups also generally divide the species by length. *Paraliparis mento* is the only species which falls between groups (II/III); its fecundity is barely high enough to place it in Group III, but its length places it in Group II. A plot of species maximum length against maximum fecundity demonstrates a significant relationship (Fig. 6), demonstrating a close relationship between maximum size of species and fecundity. Fecundity differences between species seem to reflect continuous spawning (few ripe

eggs present at once) versus periodic spawning (many ripe eggs present at once).

Great differences in numbers of ripe eggs present per female may not reflect actual yearly spawning effort. If the rate of egg development and deposition in Group I is high (i.e., on the order of two eggs per week) the total number of eggs spawned over a long period (for example, a year) could approach that of some of the periodic spawners. If a female *O. cascadiae* produces 100 eggs a year, and if a female *P. mento* spawns once a year, their yearly egg number would be similar. Thus, egg production of many species might be approximately the same, although the energy devoted to it would not necessarily be equal.

Maximum gonad weights (expressed as a percentage of total body weight) do not show differences as great as egg numbers, and are inversely related to fecundity (Fig. 7). The gonads of the "continuous" spawners are relatively larger than those of the "periodic" species. The liparids all produce large eggs; yet the large species invest relatively less energy (i.e., have relatively lower gonad:body weights) in

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reproductive products. This may be an energy saving adaptation, the result of differences in parental care, or the result of other factors differently affecting survival of offspring of large vs. small species. The abyssal benthic environment is considered to be extremely constant (Sanders, 1968; Rokop, 1974) and the benthic community is probably a stable one which is not perturbed very often. If recruitment and loss of offspring are relatively constant, extra offspring would represent an unnecessary energy loss to the adults.

Intertidal or shallow subtidal liparid species may have shorter life spans, higher fecundity and much smaller eggs than the deeper living species. Able (1973) and Able and Musick (1976) described the life history of *Liparis inquilinus*, a small (<71 mm TL), short lived (2 years) shallow water (5–97 m depth) species which probably has only one (prolonged) spawning period in its life. The mean number of large (1.0–1.3 mm) eggs present was 342 for females collected at sea (laboratory raised females had a mean of 447 eggs). Because spawning may be repetitive the total number of eggs laid by each female was unclear. Detwyler (1963) estimated that *L. atlanticus* (<97 mm SL) deposit 1,400–3,000 eggs (average size 1.1 mm) per female per season. Johnson (1969) found that *L. pulchellus* (<170 mm SL) had eggs up to 1.48 mm, but did not estimate number of ripe eggs. Eggs of other shallow water liparids are small. Aoyama (1959) found developing eggs of *L. tanakae* to be 1.7–1.8 mm. Breder and Rosen (1966) stated that eggs of *L. montagui* are about 1.1 mm and those of *L. liparis* are about 1.5 mm. De Martini (1978) stated that fertilized eggs of *L. fucensis* are about 1.0 mm.

A probable life history for deep water liparids can be constructed using new and published data. Eggs are probably laid in a protected location (such as under a rock), or in or on an invertebrate with a hard exoskeleton. Such behavior occurs in shallower living species (Able and Musick, 1976; Hunter, 1969; Parrish, 1972; Peden and Corbett, 1973). Parental care seems likely in species which lay a comparatively large number of eggs at a time, but unlikely in species laying few eggs at a time over long periods; the latter would be required to devote virtually the whole year to protecting the eggs. At least one shallow water liparid species shows parental care (Detwyler, 1963; DeMartini, 1978). Gilbert (1896) concluded that *C. ovigerum* is a mouth brooder because the holotype, a

male, held developing 4.5 mm eggs in its mouth when captured. However, ripe eggs of the species are almost 8 mm, so the holotype almost certainly ate the eggs of another species. Wenner (1979) found that the stomachs of four sexually mature male *P. garmani* contained from three to 17 undeveloped eggs of sizes similar to those occurring in possibly mature females of the same species. A male *P. calidus* was found to have eleven eggs in its stomach. Wenner suggested that *P. garmani* males may be mouth brooders, and that the eggs could have been swallowed "during ascent of the trawl." It seems more likely (if the eggs were from conspecific females) that the males were guarding the eggs. Many fishes which care for their eggs do not feed while doing so. At least one cichlid (*Pterophyllum scalare*) removes unfertilized eggs from the egg mass while caring for the eggs (Breder and Rosen, 1966). Virtual absence of stomach contents other than eggs in the above males of *P. garmani* and *P. calidus* suggests that these species may behave similarly. Egg development is probably slow because larvae from large eggs are generally very well developed at hatching. Kyûshin (1975) found that hatching *Aptocyclus ventricosus* (Cyclopteridae) had no yolk sac, and illustrations of newly hatched larvae of *Careproctus* spp. in Hunter (1969) and Parrish (1972) do not show prominent yolk sacs. If length of young at hatching is proportional to egg diameter, hatchling *C. ovigerum* (7–8 mm eggs) could be >20 mm; Kyûshin (1975) found that average length of *A. ventricosus* larvae hatched from 2.32–2.42 mm eggs was 6.7 mm, and Parrish (1972) found newly hatched *C. melanurus* to be 9–12 mm long (eggs ca. 4.5 mm). Marshall (1953) pointed out that newly hatched *Paraliparis gracilis* are well developed, and suggested that "certain species may have no pelagic stages." The young probably take up benthic residence and habits very soon or immediately after hatching. Sexual maturation may begin comparatively early, although it might take a relatively long time. All females, even those 30 mm long, examined in this study had eggs easily recognizable at 6× magnification.

This pattern of life history may be characteristic of deep sea liparids. Nielsen (1964) found that egg sizes in *Careproctus kermadecensis* (6,660–6,770 m) were distributed similarly to those of the continuous spawners discussed here. One female had about 16 eggs of 8 mm, while another had about seven 6.5 mm eggs

and a continuum of smaller egg sizes. Nielsen also examined a female *C. reinhardtii* from about 250 m depth off Greenland. He found that it contained "eggs of almost equal size . . ." which is the pattern in periodic spawners. Johnsen (1921) found that *Rhodichthys regina* from 1,738 m in the North Atlantic had about 70 eggs 3.2–4.0 mm "surrounded by many quite small eggs with a diameter up to 1 mm." Wenner (1979) captured apparently ripe male *Paraliparis garmani* in the northwest Atlantic at undisclosed depths in January, June, August and November, and female conspecifics with 3.3 mm eggs in September and January. Numbers of ripe eggs were not given. Presence of ripe males throughout the year, and presence of ripe females at widely separated times of the year may indicate continuous spawning. Abyssal and many bathyal liparid species may be continuous spawners although some bathyal and all shallow water species may reproduce periodically (possibly seasonally).

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### III. Description and occurrence of macrourid larvae and juveniles in the northeast Pacific Ocean off Oregon, U.S.A.

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**Abstract**—Although there are over 100 species of North Pacific macrourids, few of their larvae have previously been identified to species. Descriptions of postlarvae and juveniles of *Coryphaenoides acrolepis*, *C. filifer*, and *C. leptolepis* are given, with a provisional key to the identification of most species known from off Oregon. Vertical distribution of the larvae and juveniles of *C. acrolepis* apparently changes with ontogenetic development, the smallest individuals occurring shallowest. Macrourid eggs have not yet been identified from Oregon waters.

#### INTRODUCTION

LARVAE and juveniles of a few species of North Atlantic macrourids have been described, most recently by MERRETT (1978). Despite the presence of over 100 macrourid species in the North Pacific, apparently there have been no descriptions of macrourid eggs, only two descriptions of prejuveniles, and few references to identified larvae and juveniles. GILBERT and BURKE (1912) described a new genus and species *Ateleobranchium pterotum* based on a postlarval macrourid from off Kamchatka. HUBBS and IWAMOTO (1977) described postlarvae and juveniles of a new species of pelagic macrourid, *Mesobius berryi*, from off southern California and north of Hawaii. SAVVATIMSKII (1969) discussed the relationship of depths of occurrence to length of *Coryphaenoides acrolepis* (Bean) 1884 and seasonality of spawning of *C. acrolepis* and *Coryphaenoides pectoralis* (Gilbert) 1892. NOVIKOV (1970) discussed the early life history of *C. pectoralis*. Neither SAVVATIMSKII nor NOVIKOV (*op. cit.*) described the larvae or supplied a reference to such descriptions. Judging by the lack of information, MARSHALL's (1965) comment about the lack of collected specimens of larval macrourids applies particularly to the situation in the North Pacific Ocean.

This paper describes the macrourid postlarvae and juveniles collected by the School of Oceanography, Oregon State University (OSU), off the Oregon coast since 1961. The collections, made with a variety of net types during all seasons, contain 106 specimens of young macrourids. The captures have been so infrequent that only recently has sufficient material become available to allow identifications.

#### METHODS AND MATERIALS

Specimens from midwater were collected with 3.0-m and 1.8-m Isaacs-Kidd Midwater Trawls (IKMT), 2.4-m IKMT-EMPS trawls with serial opening-closing cod ends

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(PEARCY, KRYGIER, MESECAR and RAMSEY, 1977), modified Cobb trawl with EMPS cod ends (PEARCY, 1980), and 0.7-m bongo nets. Almost all the pelagic specimens were captured between 80 and 145 km off Newport, Oregon. Juveniles and adults from bottom trawls were from the collections described by IWAMOTO and STEIN (1974). Samples were preserved at sea in 10% buffered formalin-seawater solution and later transferred to 45% isopropanol for storage.

Head length was measured as the distance from the tip of the mandible in postlarvae and the tip of the snout in juveniles to the posterior tip of the opercular flap. Other measurements used are explained below.

Specimens were measured to the nearest 0.1 mm using an ocular micrometer or dial calipers. Counts follow IWAMOTO (1970). Terminology for life history stages follows HUBBS (1943).

All larvae and juveniles examined and specimens of adults used for comparative purposes are on deposit at the School of Oceanography, OSU.

#### *Characters and terminology used for identification and description*

Characters most useful in the study were premaxillary and dentary tooth patterns (useful in juveniles but not in larvae), number of rays in the first dorsal and pelvic fins, number of gas glands and retia, and pigmentation (Table 1). Pigmentation patterns proved most useful in determining conspecificity of larvae.

The study was facilitated by the relatively low number of macrourid species known from the study area (eight) and the availability of a recent review of those species (IWAMOTO and STEIN, 1974). The area considered by IWAMOTO and STEIN (1974) included the eastern North Pacific from the Bering Sea to central California. Although it is possible that larvae of species not occurring in the study area are carried into it by the prevailing currents, I consider it unlikely. Consequently, I initially assumed that larvae and juveniles captured off Oregon were conspecific with species known to occur in the same area. Because of differences in patterns of teeth in the jaws, number of swimbladder gas glands and retia, and numbers of first dorsal fin rays and pelvic fin rays, some species are easily identifiable. A complete developmental series was available for the least distinct species, *C. acrolepis*, which otherwise could have been identified only tentatively.

Macrourid larvae may be pigmented externally (on the skin surface) or internally (within myomeres, on myomeres, on the stomach or peritoneum, etc.). Internal pigment can be diffuse or composed of distinct melanophores. The distinction between internal and external melanophores may be difficult to make, as in ventral pigmentation of the stomach and peritoneum; the body wall is very thin and transparent ventrally; as a result, internal pigment appears to be external. Preservation may change intensity of pigmentation, although it does not appear to change pigment patterns. For instance, fresh specimens of juvenile *C. acrolepis* are silvery, but after preservation, they become dull.

Differences in the ratio of head length (HL) to total length (TL) are difficult to express because macrourids often lose some part of their tail when captured; the convention ordinarily used to avoid using total length is to use head length as its analog. To quantify the differences in relative body lengths among the three species described here, the horizontal diameter of the pigmented eyeball was measured, then the distance from the snout tip to the point on the tail where depth (exclusive of fin height) equalled eye diameter was measured. This distance was then expressed as number of head lengths.

Numbers of gas glands and retia are useful in identification. It is possible to identify one

Table 1. Morphological characters most useful in identifying macrourid larvae occurring or likely to occur off the coast of Oregon, U.S.A.

	<i>C. armatus</i>	<i>C. leptolepis</i>	<i>C. acrolepis</i>	<i>C. filifer</i>	<i>C. pectoralis</i>	<i>C. cinereus</i>
Body pigment	*Unknown	*Melanophores on trunk and head, closely spaced, not posterior to anal fin ~10th ray	*Melanophores on dorsum and venter, absent on last 20% of tail and on midline	*Melanophores widely scattered on dorsum around dorsal fin only	*Unknown	*Unknown
D <sub>1</sub> fin rays	8-10	8-10	9-11	11-15†	7-9	10-12
P <sub>2</sub> fin rays	10-11	9-10	8-9	9-10	6-8	8-10
Pyloric caeca	10-13	~11	12-14	8-12	12-16†	5-7
Rostral scutes	Absent	Absent	Strong†	Strong†	Absent	Strong†
Size at which pectorals normalize	<18.2 mm HL	6.2-15.0 mm HL	9.4-9.8 mm HL	14.1-14.6 mm HL	—	—
Precaudal vertebrae	13-15	12	14-15	—	13-14	13-14
Gas glands	5-6	6	4	4	2	4
Retia	5-6	6	4	4	2	4

\* Larval character. † Adult/juvenile character.

species (*C. pectoralis*) solely by its possession of two gas glands. The swimbladder is present and apparently functional at 1.5 mm HL in at least one species, *C. rupestris* (Gunnerus), 1765 (MERRETT, 1978). All specimens examined in the study were larger than 1.8 mm HL. The swimbladder in postlarvae and juveniles is easily reached through an incision in the side of the abdominal cavity, and its careful examination or excision results in little damage to the specimen.

For purposes of description here, the transition from larva to juvenile is called metamorphosis; it seems to be rapid, and there is only a small difference in head lengths between premetamorphic and postmetamorphic individuals of both *C. acrolepis* and *C. filifer* (Table 1). The most important morphological change at this time is the loss of the pectoral fin peduncle and appearance of the adult pectoral fin form. Simultaneously, the mouth, formerly at a distinct angle, becomes horizontal, the snout becomes distinct, and the stomach is reduced in prominence, decreasing the depth of the posterior part of the trunk. Stomach prominence may be a function of feeding habits. Larvae are commonly found with the stomach crammed with food, but juveniles are not. The phenomenon may be a partial cause of the very different appearances of larvae and juveniles.

## RESULTS AND DISCUSSION

### *Larval diagnosis and development*

*Coryphaenoides acrolepis* (Fig. 1). This is the only species examined of which a complete developmental specimen series was available. The characters most important in identification were number of first dorsal fin and pelvic fin rays, number of gas glands, and presence of rostral scutes in juveniles greater than about 16 mm HL (Table 1). Pigment pattern enabled definite determination of conspecificity of small individuals lacking rostral scutes with larger specimens having them. All 78 individuals examined have a distinctive pigment pattern in which the entire body is internally or externally pigmented except the last part of the tail, which abruptly becomes internally unpigmented. The fraction of the body that is pigmented is quite consistent; HL represents 27.8 to 34.2% of the pigmented length (PL). The fraction does not vary with size of individual. A linear regression of HL versus PL is highly significant ( $HL = 0.08 + 0.30 PL$ ;  $r^2 = 0.97$ ). The distinct character, seen in juveniles and in the smallest individual studied (1.8 mm HL), is unaffected by period of preservation and is clearly not a preservation artifact.

As in all known macrourine larvae, a peduncular pectoral fin is present and well developed. It disappears between 9.4 and 9.8 mm HL, at which time the 'normal' adult pectoral appears. All other fins have their full complement of rays by 3.8 mm HL.

### 1.8 mm HL (Fig. 1A)

Individuals of this size may be recently hatched; ripe eggs of *C. acrolepis* are at least 2.0 mm in diameter (observations of STEIN and PEARCY). The dorsal and anal fins are not developed; the pelvic fins are well developed. Stellate chromatophores form a bilaterally symmetrical patch on the frontal region of the head; the lower jaw is completely but sparsely pigmented. Very small, scattered melanophores occur along the bases of the dorsal and anal finfolds; they are especially noticeable on the posterior part of the caudal region. Extensive internal pigmentation is present within the myomeres and on the peritoneum. Myomeric pigment is absent from the posterior part of the tail.

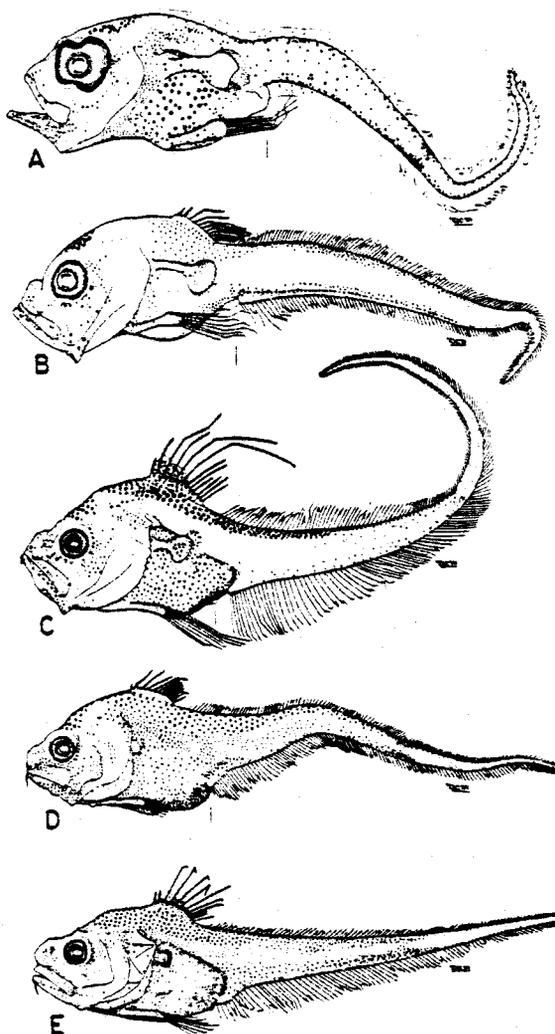


Fig. 1. *Coryphaenoides acrolepis*. A: 1.8 mm HL; B: 3.8 mm HL; C: 6.7 mm HL; D: 9.8 mm HL; E: 12.5 mm HL.

#### 3.8 mm HL (Fig. 1B)

Frontal pigment has increased and become divided into two similar oval patches, one on each side of the head. The lower jaw is pigmented except for the anterior part of the gular region. Pigment along the bases of the median fins is still present, but it is not so prominent posteriorly. Internal pigmentation is as above.

#### 4.7 mm HL

The anterior dorsal melanophores have become larger and denser, forming a longitudinal dorsal patch reaching from the first dorsal fin spine posteriorly to about half the length of the fish. The anterior part of the gular region remains unpigmented.

*6.7 mm HL (Fig. 1C)*

Pigmentation has become much more extensive. The dorsal pigment extends from the nuchal region to the caudal end of the myomeric pigment and onto the first dorsal fin. Ventral melanophores are present but sparse on the caudal region. Peritoneal melanophores are evenly distributed; external pigment is sparse on and around the bases of the pelvic fin rays and is quite dense around the anus. Pigment is scattered on the suborbital and postorbital regions. The anterior part of the gular region remains unpigmented. The mandibular barbel is present as a small, broad-based flap or bump.

*7.4 mm HL*

Dorsal and ventral pigmentation is extensive, composed of large and small pigment spots coalescing in the trunk area below the first dorsal fin. The basipterygia are completely pigmented, and the pigment around the anus is not so dense as at 6.7 mm HL. The anterior part of the gular area remains unpigmented; a broad band following the lateral line down the sides of the tail is externally unpigmented but is evenly pigmented internally.

*9.4 mm HL*

The area along the lateral line is sparsely pigmented externally, and trunk pigment is more extensive; internal myomeric pigment is more prominent in the previously unpigmented caudal region. The dorsal pigment now extends to the frontal region, and the previously unpigmented part of the gular region of the lower jaw is smaller, although its anteriormost third remains pigment free. The pectoral fins are still peduncular, and the barbel, although distinct, is quite short.

*9.8 mm HL (Fig. 1D)*

Metamorphosis has occurred, although the stomach is still relatively larger and more swollen than in later juveniles. The unpigmented caudal region has some internal pigmentation consisting of distinct melanophores and diffuse myomeric pigment, is very lightly pigmented along the fin bases, and remains distinct. The lower jaw is completely pigmented. The pectorals are adult in form, although their bases form small lobes. The barbel is slender, short, and lightly pigmented.

*12.5 mm HL (Fig. 1E)*

The body is covered with small punctate melanophores evenly distributed except along the lateral line, where they are relatively sparse. The transition between internally pigmented and unpigmented caudal regions is less abrupt. The peritoneum, which can be seen through the body wall, is uniformly darkened. The barbel is fully developed.

*15.3 mm HL*

The adult body form is clearly present; the stomach is not swollen as it was previously. At this size, the distinctive pigment-free caudal region cannot be clearly distinguished from the remainder of the tail.

*16.6 mm HL*

The rostral scutes and scales begin to form.

*Coryphaenoides leptolepis* (Günther) 1877 (Fig. 2D, E). Although the eight specimens

## Macrourid larvae and juveniles in the northeast Pacific Ocean off Oregon

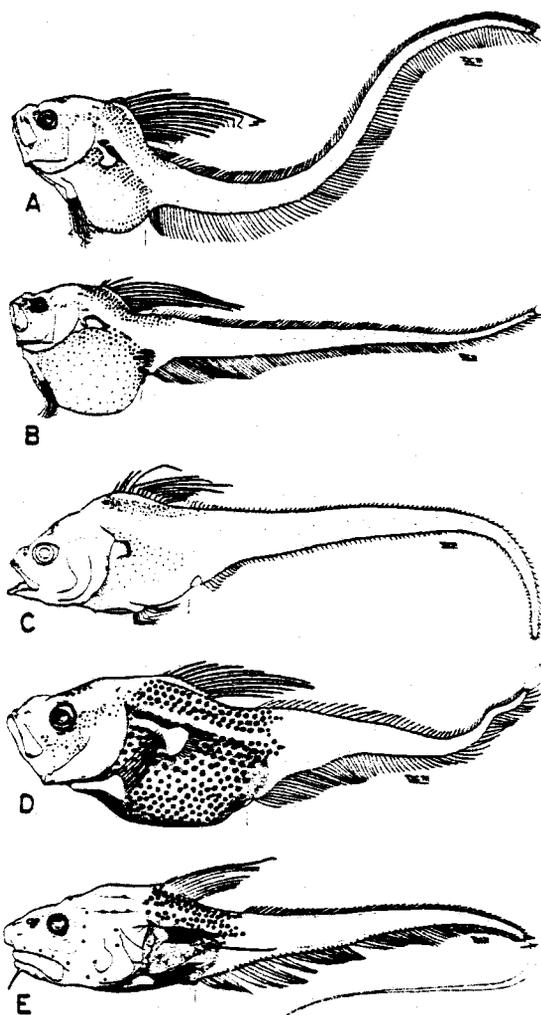


Fig. 2. *Coryphaenoides filifer*. A: 6.4 mm HL; B: 10.5 mm HL; C: ~14.6 mm HL (a composite from two damaged specimens). *Coryphaenoides leptolepis*. D: 6.2 mm HL; E: 15.2 mm HL. Posterior of caudal not drawn, although present, in E.

available do not form a complete series, they are clearly conspecific and allow description of important characters and of several growth stages. The characters most important in identification were pigment pattern, number of gas glands, and number of first dorsal and anal fin rays (Table 1). The pigment pattern is present even in relatively large juveniles; it provided the connection between juveniles identifiable using adult characters and smaller individuals not so identifiable. In all specimens up to at least 19.6 mm HL (> 84 mm TL), evenly scattered pigment spots occur on the trunk from just anterior to the dorsal fin posterior to about the 10th anal fin ray. The pigment spots are visible even in specimens darkened by preservation. Posterior to the 10th anal ray no comparable pigment is present. The pigmented area is sharply distinct from the rest of the tail.

All fins other than the pectorals are fully developed by 5.9 mm HL. The pectorals are peduncular and paddle-like distally. The peduncular fin is lost between 6.2 and 13.6 mm HL, at which size a fully developed adult form of pectoral fin is present.

#### 5.9 mm HL

Clearly separated melanophores are dense on the trunk and stomach. Some melanophores are evenly distributed over the frontal region of the head, and a few are present on the ascending processes of the premaxillae. Pigment is present around the basipterygia and under them on the stomach, visible through the body wall. A wide notch between the anteriormost teeth is present at the tip of the premaxillaries.

#### 6.2 mm HL (Fig. 2D)

Trunk pigmentation is less dense than at 5.9 mm HL; it is composed of evenly distributed stellate melanophores. Peritoneal pigmentation is denser anteroventrally and posterodorsally. The large and small punctate frontal melanophores form a bilaterally symmetrical heart-shaped pattern with the apex pointing posteriorly. A narrow band of internal melanophores on the head extends in an arc from the suborbital region to above the opercle. Dense black punctate melanophores are present on the peritoneum under the unpigmented basipterygia.

#### 15.2 mm HL (Fig. 2E)

Metamorphosis has occurred. The trunk melanophores are relatively larger, blotchier, and more widely separated than in the postlarval stages. The adult form of pectoral fin is present. The light brown body is fully scaled. The trunk melanophores make the body anterior to about the 10th anal fin ray appear blackish.

#### 19.6 mm HL

Trunk melanophores are still present although they have become large, blackish, widely separated spots. Fish at this size are easily identifiable by using keys to adults.

*Coryphaenoides filifer* (Gilbert) 1895 (Fig. 2A, B, C). The 10 available specimens do not form a complete series but are clearly conspecific. Characters most useful in identification of *C. filifer* were number of first dorsal fin rays, pelvic fin rays, gas glands, and pigment pattern (Table 1). The species can be distinguished from all others likely to be captured off Oregon by the abundance of the rays in the first dorsal fin. One larval individual, identical in other respects to the other specimens identified as *C. filifer*, had 15 first dorsal fin rays. The highest previously reported ray number was 14 (IWAMOTO and STEIN, 1974). The pigment pattern allowed identification of individuals with 11 or 12 first dorsal fin rays. The specimens might otherwise have been confused with *C. acrolepis* or *C. cinereus* (Gilbert) 1895. The distinct pigment pattern in all postlarvae and juveniles examined consists of a 'dorsal oval' of melanophores surrounding the first dorsal fin; its long axis parallels the length of the fish. The dorsal oval generally extends anterior to the first dorsal fin, posteriorly to about the 12th ray of the second dorsal fin, and ventrolaterally as far as the lateral line. The peritoneum is distinctly pigmented dorso-laterally. There are scattered small melanophores along the lateral line and on the gular and suborbital regions of the head.

All fins except the pectorals have their full complement of rays in the smallest specimen examined (6.4 mm HL). Metamorphosis occurs at a greater HL (between 14.1 mm and 14.6 mm) than in either *C. acrolepis* or *C. leptolepis*.

The species is distinctly longer at any given head length than are either of the other two species; total lengths of the two specimens that had lost the least amount of caudal were 6.7 times HL (at 6.4 mm HL) and 6.9 times HL (at 11 mm HL). The distance from the snout to

where the caudal fin is equal in depth to the horizontal diameter of the pigmented eyeball ranges between 3.5 and 4.6 times head length, whereas for *C. leptolepis* the range is 2.4 to 2.7 and for *C. acrolepis* it is 1.8 to 2.4.

6.4 mm HL (Fig. 2A)

The melanophores forming the dorsal oval are small, punctate, dense black or dark brown, and closely spaced. Pigment is abundant on the dorsolateral surface of the peritoneum but not on the ventral surface, possibly because the stomach of the specimen is greatly swollen with food. There are a few tiny melanophores on the ventral surfaces of the lower jaw. On each frontal is an oval patch of small, widely separated stellate melanophores.

10.5 mm HL (Fig. 2B)

The melanophores forming the dorsal oval and stomach pigmentation are much larger and less dense, forming relatively large spots that tend to coalesce. A few small pigment spots are present on the isthmus and the ventral margin of the opercular opening, along the lateral line, and on the posteriormost part of the caudal. Apparently neither number nor size of pigment spots increases on the frontal surfaces of the head or ventral surfaces of the lower jaw or the stomach.

~14.1 mm HL (damaged)

Metamorphosis starts to occur at about 14 mm. Relative to smaller specimens, the angle of the mouth is nearer the horizontal, the stomach is smaller, the posterior part of the trunk is not so deep and is about equal in depth to the anterior part of the tail. The peduncular pectoral fin is still present and well developed.

~14.6 mm HL (damaged) (Fig. 2C)

Metamorphosis is almost complete. The dorsal oval is still distinct. Both available specimens near this size are in poor condition, precluding further descriptions of pigment patterns. The pedunculate pectoral fin has disappeared and the fully developed adult form of pectoral fin is present.

~16 mm HL (damaged)

Similar to 14.6 mm specimens. Pigmentation differs in the presence of small dark brown pigment dots over the entire body, especially on the tail, forming diffuse lengthwise bands above, below, and along the lateral line.

*Coryphaenoides armatus* (Hector) 1875. No larvae or postlarvae of this species, the most abundant macrourid occurring off Oregon (observations of PEARCY, STEIN and CARNEY), were identified. One juvenile (18.2 mm HL) was collected by IKMT between the surface and 2520 m in 3909 m of water. The specimen was clearly of adult form and was easily identified. Metamorphosis thus occurs in *C. armatus* by this size, and judging by the complete squamation of the specimen, it probably occurs at some significantly smaller size.

*Provisional key to postlarvae and juveniles of Coryphaenoides occurring off Oregon*

- A. Pyloric caeca 5-7 (first dorsal fin rays 10-12, pelvic fin rays 8-10) . . . . . *C. cinereus*  
 AA. More than 9 pyloric caeca . . . . . B  
 B. Gas glands and retia 2; 6-8 pelvic fin rays . . . . . *C. pectoralis*

BB.	Gas glands and retia 4-6; 8-10 pelvic fin rays . . . . .	C
C.	Gas glands and retia 4 . . . . .	D
CC.	Gas glands and retia 5-6 . . . . .	E
D.	Pyloric caeca fewer than 11; first dorsal fin rays 11-15; pelvic fin rays 9-10. Pigment generally confined to dorsum, forming an oval surrounding dorsal fin base; melanophores sparse, well separated . . . . .	<i>C. filifer</i>
DD.	Pyloric caeca 12-14; first dorsal fin rays 9-11; pelvic fin rays 8-9. Body and tail pigmented except for last part of tail; pigmented length 2.9-3.6 times HL . . . . .	<i>C. acrolepis</i>
E.	Trunk with large dark pigment spots posteriorly to about 10th anal fin ray, up to at least 20 mm HL; 12 precaudal vertebrae; gas glands and retia 6. Premaxillary teeth forming a wide inner band of small teeth with an outer enlarged series . . . . .	<i>C. leptolepis</i>
EE.	Trunk pigment not as above; 13-15 precaudal vertebrae; gas glands and retia 5-6. Premaxillary teeth biserial or irregularly biserial . . . . .	<i>C. armatus</i>

The key is based upon available specimens and should be considered provisional. Two rare species [*C. yaquinae* (IWAMOTO and STEIN, 1974) and *Nezumia stelgidolepis* (Gilbert) 1891] have been omitted. Although postlarvae of only three of the six species included have been identified and described, it seems reasonable to use the adult characters that proved useful in identification of larvae of the three species for all seven species. Such a key may be useful to future studies by distinguishing other larvae found in the same waters from the three species described here. Hopefully, it will also stimulate examination of previously unexamined macrourid larvae in other collections.

#### *Abundance and vertical distribution*

To see whether juveniles avoid small nets, I compared relative abundances of all *C. acrolepis* juveniles captured in midwater in the OSU collections; they were captured with two kinds of nets (IKMT and Cobb trawl). The effects of factors such as seasonal abundance, distance offshore, and depth of capture on relative abundances and distribution could not be determined. Captures of larvae and juveniles were too rare, even after pooling, to allow separate analyses on these bases. Net size affected catch rates; a small (50 m<sup>2</sup>) opening-closing Cobb trawl (PEARCY, 1980) yielded almost 50 juvenile *C. acrolepis* in four hauls at 500 to 600-m depth during one cruise. However, the number of individuals (10<sup>6</sup> m<sup>3</sup>)<sup>-1</sup> was even lower than for individuals captured by 1.8-, 2.4-, and 3-m IKMT's. Values for IKMT captures average 18.8 individuals (10<sup>6</sup> m<sup>3</sup>)<sup>-1</sup>, and for Cobb trawl captures average 8.9 individuals (10<sup>6</sup> m<sup>3</sup>)<sup>-1</sup>. The larger (18 vs 6 mm) mesh size of the Cobb trawl may explain the relatively lower catches.

The rarity of macrourid larvae, postlarvae, and juveniles is a puzzle that has been often discussed but remains unresolved (e.g. JOHNSEN, 1927; MARSHALL, 1965, 1973; MERRETT, 1978). The collections for this study were from over 2700 midwater trawl hauls, many of which (~900) were with multiple opening-closing nets, and thus are the equivalent of 5000 to 6000 separate tows. Yet relatively few specimens in any of the three developmental stages were captured. Of these, none was a prolarva, some were postlarvae, and most were juveniles.

Vertical distribution of early growth stages of two of the three species studied here is generally unknown. Most of our specimens of *C. filifer* and *C. leptolepis* were captured

before we began to use opening-closing midwater trawls and thus the depth of their capture cannot be stated definitely. SAVVATIMSKII (1969) reported *C. acrolepis* 10 to 15 mm TL occurred at 100 to 200 m. The specimens of *C. acrolepis* show a pattern of vertical distribution (Fig. 3) that supports the general pattern postulated by MARSHALL (1965) and apparently given, but not cited, by SAVVATIMSKII (1969) and recently supported by MERRETT (1978). The four smallest specimens of *C. acrolepis* ( $\leq 6.7$  mm HL) were captured between the surface and 200 m. All but one of the remaining specimens (73) were captured in tows reaching 500 m or deeper. In a series of day and night horizontal tows from 2 to 5 September 1978, at depths of 500, 650, 800 and 1000 m, with a 50 m<sup>2</sup> opening-closing Cobb trawl net, juvenile *C. acrolepis* were captured only in nets fished at 650 to 800 m; postlarvae were collected at 500 m. In general, of all specimens examined for this study, those less than 6.7 mm HL occurred at 200 m or less, those of about 7.3 to 15.6 mm HL at 600 m or less, those 9.8 to 18.0 mm HL between 500 and 800 m; only individuals greater than 13 mm HL occurred below 800 m. This the sparse data generally support the hypothesis of ontogenetic migration of subadult macrourids off Oregon.

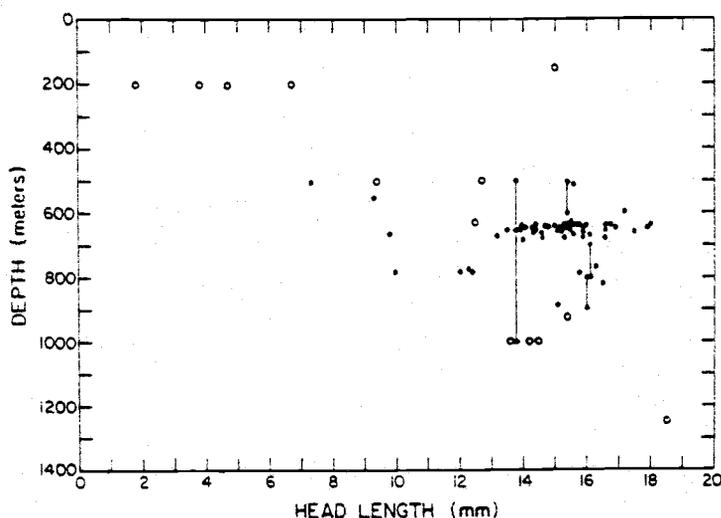


Fig. 3. Depth of capture vs head length for *C. acrolepis*. ○: maximum depth of capture by non-closing net; ●: depth of capture by opening-closing net. Vertical lines represent depths of single captures in oblique hauls by opening-closing nets, where change in depth was  $\geq 100$  m.

The results complement the work of MULCAHY, KILLINGLEY, PHLEGER and BERGER (1979), who analyzed ratios of oxygen and carbon isotopes in otoliths of *C. acrolepis*. They concluded that *C. acrolepis* undergoes an ontogenetic migration "of at least 1400 m" "early in the life cycle", based on decreasing estimated temperatures of 6 to 2°C at times of otolith deposition. The temperatures of the water in which the specimens examined in this study were captured ranged from 1.7 to 8.1°C. Specimens less than 6.7 mm HL collected at 200 m or less were all in water of 6.6°C or warmer (unpublished OSU data report and *in situ* temperature sensor on trawls).

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*Note added in proof*—Since this paper went to press, examination of additional specimens of *C. armatus* has shown that some small benthic juveniles, but not all, have trunk pigmentation similar to that of *C. leptolepis* postlarvae. As noted above, the only pelagic juvenile captured of *C. armatus* lacks such pigment. Consequently, identifications of larvae as *C. leptolepis* should stand as described for the present, but must be considered as provisional pending availability of more material.

IV. ASPECTS OF REPRODUCTION, EARLY LIFE HISTORY, AND BIOLOGY  
OF BATHYAL AND ABYSSAL MACROURID FISHES OFF OREGON, U.S.A.

David L. Stein and William G. Pearcy

ABSTRACT

Despite the abundance of bathyal and abyssal macrourids in the North Pacific Ocean, little is known about their biology. This paper describes the egg sizes, fecundities, times of spawning, early benthic life, size frequency, and distribution by sex and size of the four most common macrourid species off Oregon: Coryphaenoides acrolepis, C. armatus, C. filifer, and C. leptolepis.

Sizes of eggs of comparable developmental stages from different species were quite different. Average fecundities ranged from about 26,000 to 2,500,000 eggs. Two species, C. acrolepis and C. filifer, apparently spawn semi-annually; ripe females of C. armatus and C. leptolepis were not collected. Juveniles of the three sympatric species, C. armatus, C. filifer, and C. leptolepis, become benthic in habit at different sizes; C. filifer is largest. Different mouth size of each species may minimize competition for food.

Size frequency distributions were either unimodal (C. filifer, C. armatus) or bimodal (C. acrolepis, C. leptolepis). However, small C. filifer were rarely collected, and small C. armatus were relatively common, suggesting that small C. filifer remain pelagic longer than the young of other species. C. armatus and C. leptolepis were "bigger-deeper," but this trend was not evident in the other two species.

Sex ratios also differed: male C. armatus and C. leptolepis were much less abundant than females, although their proportion increased with distance offshore. Numbers of males and females were about equal in C. acrolepis and C. filifer; no trends were evident. Little evidence for the existence of sexual aggregation was found.

The liver apparently serves as a buoyancy mechanism in large C. armatus.

Macrourids are possibly the single most important family of deep-sea benthic fishes, both in terms of diversity and of biomass (Hubbs, 1954). Certainly the second is true in the northeast Pacific Ocean (Pearcy, Stein, and Carney, unpub.), where macrourids often form close to 100% of the total catch by weight and by numbers at depths below 2000 m. Yet, little is known about macrourid biology. The most is known about North Atlantic and Mediterranean species. Rannou (1975, 1976), Rannou and Thiriou-Quievreux (1975), Motais (1960), Geistdoerfer (1973, 1975, 1977, 1979a, 1979b), Haedrich and Polloni (1976), Ibañez (1977), Johnsen (1921, 1927), Macpherson (1979), Marshall (1965, 1973), Merrett (1978), Savvatimskii (1969, 1971a, 1971b), Savvatimskii, Kokh and Ernst (1977), Sedberry and Musick (1978), Gordon (1979a, 1979b) and other, earlier authors have studied aspects of the biology of such macrourids. In contrast, much less is known about the biology of North Pacific macrourids. Brothers, Mathews and Lasker (1976) studied daily growth rings in the otoliths of Coryphaenoides acrolepis (Bean); Matsui and Rosenblatt (Scripps Institution of Oceanography, 1975) have studied reproduction and distribution in the same species. Novikov (1970) described aspects of the life history, population structure, diet, growth, and distribution of C. pectoralis (Gilbert) in the Bering Sea. Kulikova (1957) investigated the age and growth of several North Pacific macrourids (C. pectoralis, C. cinereus (Gilbert), C. angustifrons Rass). Okamura (1970a, 1970b), in his taxonomic reviews of Japanese macrourids, included short accounts of the biology of some species. These accounts, by their brevity and rarity, serve to indicate the present state of knowledge about the biology of Pacific grenadiers.

Members of the School of Oceanography, Oregon State University, have sampled the continental slope and abyssal plains off Oregon and farther west from 1963 to 1976 (Table 1). Specimens used in this study were obtained from these areas (Fig. 1, Fig. 2). Although the sampling program was not designed specifically to investigate the biology of deep benthic fishes, enough samples (579) and specimens (4852) were collected over a long enough period to allow study of certain aspects of the biology of four species of Oregon macrourids. These aspects

Table 1. Number of trawls which captured macrourids, by depth and month.

	<u>Jan</u>	<u>Feb</u>	<u>Mar</u>	<u>Apr</u>	<u>May</u>	<u>June</u>	<u>July</u>	<u>Aug</u>	<u>Sept</u>	<u>Oct</u>	<u>Nov</u>	<u>Dec</u>	<u>Total</u>
200-2000 m	5	1	1	5	-	3	3	1	2	7	1	1	30
2000-3000 m	15	24	20	7	10	8	13	8	12	14	3	2	136
over 3000 m	<u>1</u>	<u>-</u>	<u>-</u>	<u>-</u>	<u>2</u>	<u>7</u>	<u>1</u>	<u>7</u>	<u>-</u>	<u>10</u>	<u>-</u>	<u>-</u>	<u>28</u>
	21	25	21	12	12	18	17	16	14	31	4	3	194

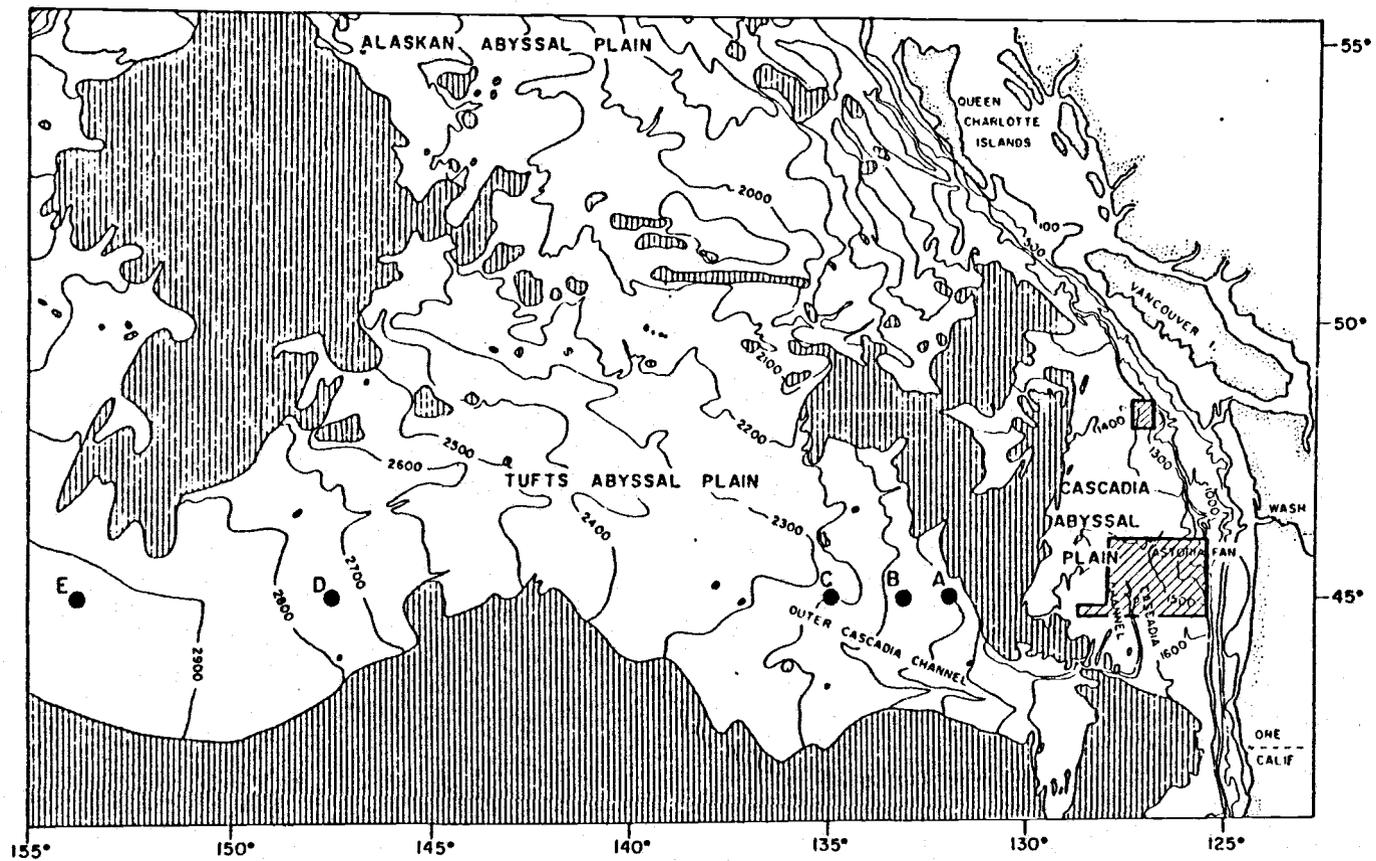


Figure 1. Northeast Pacific Ocean, showing study areas and stations (from Percy, Stein and Carney, unpublished).

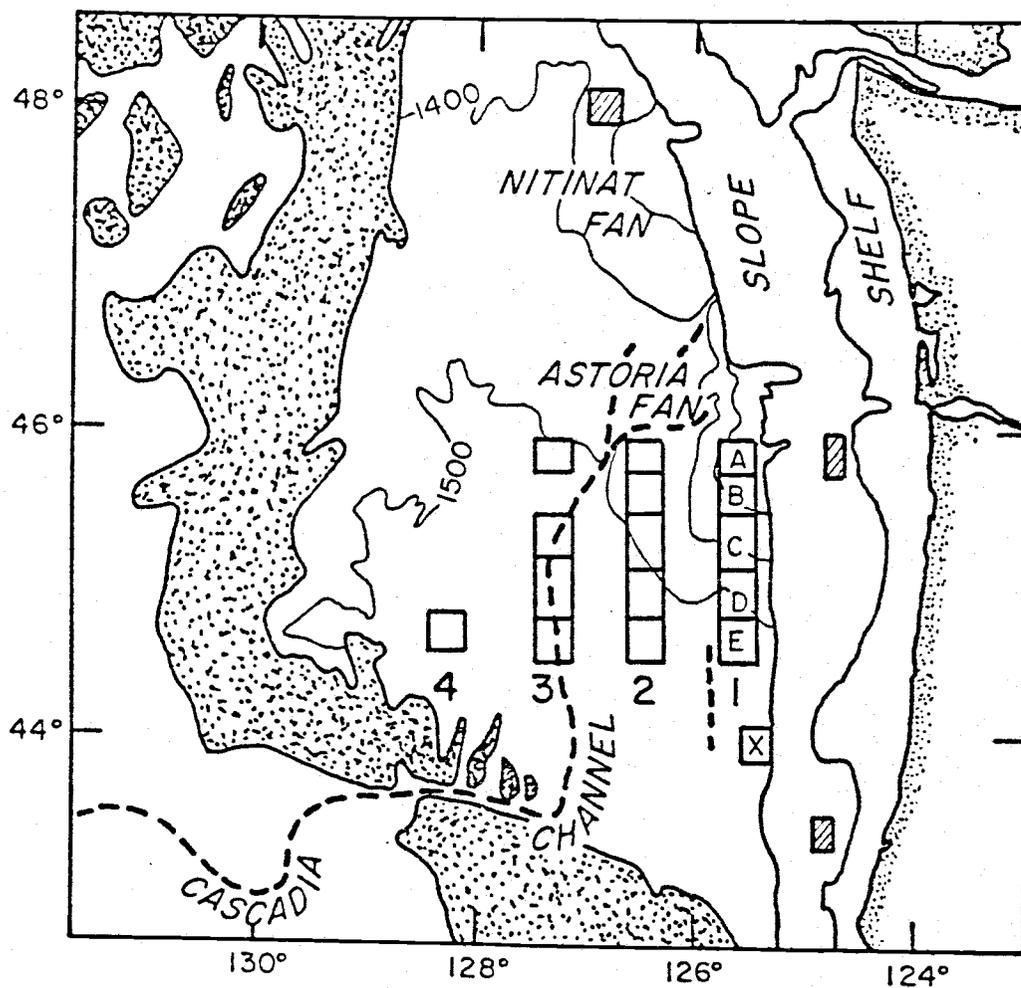


Figure 2. Stations sampled on Cascadia Abyssal Plain (from Percy, Stein and Carney, unpublished).

include food habits (Pearcy and Ambler, 1974); early life history (Stein, 1980), distribution and abundance (Pearcy, Stein, and Carney, unpublished) and this paper, reproduction, early life history, length-weight relationships and population structure.

### Study Area

These areas have recently been described by Pearcy, Stein and Carney (unpublished). This description will consequently be brief. The continental slope off Oregon and Washington begins at depths of about 146 m. It often has a steep gradient ( $2^{\circ}$ - $35^{\circ}$ ) which results in great depth changes occurring over relatively short distances. Because of the presence of rock outcrops and uneven bottom topography (Maloney, 1965) large areas of the slope cannot be sampled by trawls.

Farther west, there are two abyssal plains: Cascadia Abyssal Plain and Tufts Abyssal Plain (McManus, 1964). The former is adjacent to the continental slope, and is bordered by submarine ridges on the west (the East Pacific Rise) and south (Mendocino Fracture Zone; Juan de Fuca and Gorda Ridges) (Fig. 1, Fig. 2). Two large Pleistocene fans, the Astoria and Nitinat Fans, produce a pronounced slope to the south. Consequently, depths on Cascadia Plain increase from 2100 m near the northern slope base to about 3000 m near the southern end of the plain (Hurley, 1960; Nelson, 1968). Thus, depths on Cascadia Abyssal Plain increase to the south at constant distance from land, and from east to west with increasing distance from land.

Tufts Abyssal Plain is farther offshore (Fig. 1, Fig. 2). It is much larger than Cascadia Plain, and also less well defined. Its borders are the East Pacific Rise on the east, and hilly seamounts to the south. It is not well defined to the north (from the Alaskan Abyssal Plain) or to the west (from the Aleutian Abyssal Plain). Depths on Tufts Plain range from about 3000 m in its eastern portion to about 5300 m in the westernmost region.

From east to west on both the slope and the abyssal plains, sedimentation rates decrease, proportion of radiolarians and clays in the sediments increases, occurrence of plant material and detritus decreases

(Griggs, Carey and Kulm, 1969; Nelson, 1968), organic carbon decreases (Gross, Carey, Fowler and Kulm, 1972). In general, there is also a decrease in benthic biomass from east to west of both invertebrates (Carey, 1965; Pereyra and Alton, 1972) and fishes (Alton, 1972; Pearcy, Stein and Carney, unpublished).

## MATERIALS AND METHODS

The macrourids used for this study were from the collections described by Iwamoto and Stein (1974) and Pearcy, Stein, and Carney (unpublished). The fishes were collected by 3-m beam trawl and 7 and 13-m otter trawls. Slope collections were made mainly by otter trawl, while abyssal plain collections were usually made using the beam trawl. Depths sampled ranged from less than 400 m (shallowest capture of a macrourid using bottom trawls) to 5180 m. The deepest samples were obtained on the western edge of Tufts Abyssal Plain, 2225 km west of the Oregon coast. A total of 4212 macrourids was examined for this study: 308 C. acrolepis, 2929 C. armatus (Hector), 1261 C. filifer (Gilbert), and 354 C. leptolepis (Günther). Several other species (Nezumia stelgidolepis (Gilbert), C. pectoralis, C. cinereus, C. yaquinae Iwamoto and Stein) were collected, but were too few (2-30 individuals) to permit analysis.

The relationships of fish weight to length, and of length, weight, sex, and (in females) reproductive condition to season, depth, latitude, and longitude, by species, were studied using the Statistical Interactive Programming System (SIPS) at Oregon State University.

Fishes were preserved at sea in 10% formaldehyde-seawater solution. When ashore, they were identified, total length (TL) measured to the nearest millimeter (mm), and weighed to the nearest gram (gm) after draining for several minutes. Individuals in which the tail was obviously broken or regenerated were noted. TL of individuals with broken or regenerated tails was estimated from head length:TL relationships obtained from measurement of intact specimens. The sex of each individual was determined by gross examination, after which, if the specimen was female, the ovaries were removed, blotted, and weighed together to the nearest 0.1 gm. Each ovary was then examined, and the stage of the eggs contained in it was determined by the following criteria, which are common to all species examined.

- Stage I: eggs small, .11-.50 mm diameter, containing a definite, distinct core, with the perivitelline space about equal to the diameter of the core. Eggs firmly bound in ovarian tissues.
- State II: eggs .21-.90 mm diameter, perivitelline space much narrower than diameter of core, some yellowish yolk present. Eggs firmly bound in ovarian tissues.
- Stage III: eggs .41-1.60 mm diameter, translucent, yolky, filled with many small oil droplets; center of egg sometimes clearly visible. Eggs loosely held in ovarian tissues.
- Stage IV: eggs large, up to 2.20 mm diameter, translucent, yellow, yolky, a single large oil droplet located peripherally. Eggs free in ovary.
- "Ripe."

Although the ovaries of individual females differed from each other in size, both always contained eggs at the same stage of development. The number of eggs per female was estimated by weighing both ovaries, then removing three samples of eggs of equal weights from the anterior, middle, and posterior of one ovary. Choice of ovary was random. Average number of Stage III or Stage IV eggs per gram was calculated (Stage I or II eggs are more likely to be resorbed) and used to compute the total number of ripening or ripe eggs in each ovary pair. Unripe eggs present were uniformly distributed throughout the ovary. The number of ovaries weighed or from which eggs were measured is given in Table 2. Egg sizes for all species at all developmental stages collected are given in Table 3.

Gonadal index (Motais, 1960) computed as total ovary weight/total fish weight x 100, was calculated for females in which the ovaries contained eggs which were all clearly of the same non-transitional stage of development.

Sex ratios were calculated as percent males per tow.

Table 2. Number of ovary pairs examined, by species, including number in which eggs were measured and number of ovary pairs weighed to compute gonadal indices.

	<u>No. in which eggs were measured</u>	<u>No. weighed</u>
<u>Coryphaenoides acrolepis</u>	33	87
" <u>armatus</u>	71	452
" <u>filifer</u>	173	594
" <u>leptolepis</u>	<u>27</u>	<u>104</u>
Total	304	1227

Table 3. Size ranges of eggs at each developmental stage collected, for Coryphaenoides acrolepis, C. armatus, C. filifer, and C. leptolepis.

Stage	I	II	III	IV
<u>Coryphaenoides acrolepis</u>	.11-.30	.31-.60	.81-1.60	2.01-2.10
" <u>armatus</u>	<.20	.21-.40	.41- .60	>.60?
" <u>filifer</u>	.11-.50	.31-.90	.71-1.60	1.61-2.20
" <u>leptolepis</u>	.11-.30	.21-.50	----	----

Entire livers were removed from 36 C. filifer from 123 to 670 mm TL, and from 77 C. armatus from 135 to 879 mm TL, and weighed to the nearest 0.1 mg. Relationships of liver weight to individual length and weight, season, sex, and reproductive condition were examined. Specimens are on deposit at the California Academy of Sciences.

## RESULTS

Reproduction

Ripe females of only two species, C. acrolepis and C. filifer, were collected. However, a few Stage III C. armatus were captured. No female C. leptolepis with eggs developed beyond Stage II were captured.

Ripe female C. acrolepis were captured only in April and September; ripe and spent females were collected in October (Fig. 3). The gonadosomatic index was proportional to egg development - the riper the eggs, the higher the index (Table 4). Females mature at about 460 mm TL, the shortest length at which Stage III eggs occur. Fecundity estimates varied widely (22,657 to 118,612, mean 70,025) (Table 5). Fecundity may be related to length but our sample was too small (7) to show such a relationship.

Female C. filifer with ripe eggs were collected in January, June, July, and August (Fig. 3). The ripest females captured at those times had large, well-developed Stage IV eggs, free in the ovary. A few spent females were collected in February and in June. Many of the ovaries from females collected at other times contained a few atretic Stage IV eggs and large numbers of Stage II eggs. Gonadosomatic index is related to egg development as in C. acrolepis (Table 4). Minimum TL of mature females is about 500 mm. Fecundity varies widely (9500 to 51,110, mean 25,976) (Table 5) and is directly related to total length (Fig. 4).

Although C. armatus was the most abundant macrourid in the collections, few females had maturing eggs, and none was ripe. This is reflected in the relatively small number of ovaries from which eggs were measured (Table 2). Maturity may occur in sizes much larger than in C. acrolepis and C. filifer; the only females with ripening eggs were more than 700 mm TL. Fecundity estimates of the Stage III eggs of two of the largest females captured (793 and 866 mm TL) were about 2,500,000 eggs per female (Table 5), although it is not known whether all eggs at that stage develop to maturity. At similar developmental stages, eggs of C. armatus are much smaller than those of C. acrolepis and C. filifer (Table 3).

Table 4. Means and ranges of gonadosomatic indices (G.I.) and number of specimens examined for all three species (C. acrolepis, C. filifer, and C. armatus) from which ripe or ripening eggs were collected.

	<u>C. acrolepis</u>			<u>C. filifer</u>			<u>C. armatus</u>		
	<u>Mean G.I.</u>	<u>Range</u>	<u>N</u>	<u>Mean G.I.</u>	<u>Range</u>	<u>N</u>	<u>Mean G.I.</u>	<u>Range</u>	<u>N</u>
Stage I	0.5	0.1-1.5	44	1.2	0.3-2.3	57	0.2	0.1-0.5	67
Stage II	1.4	0.4-1.9	10	1.5	1.0-2.1	18	1.5	1.1-2.0	4
Stage III	5.3	1.7-8.0	9	5.0	1.7-11.4	48	5.6	2.8-8.7	4
Stage IV	13.7	12.8-14.5	2	9.7	6.1-14.6	7	---	---	--

Table 5. Fecundities, total lengths, and number of specimens examined of Coryphaenoides acrolepis, C. armatus, and C. filifer.

	<u>Fecundity</u>	<u>Total Length</u>	<u>N</u>
<u>Coryphaenoides acrolepis</u>	70,025 (22,657-118,612)	685 (534-842)	7
" <u>armatus</u>	2,585,374 (2,459,330-2,711,398)	829 (793-866)	2
" <u>filifer</u>	25,976 (9,034-51,110)	593 (480-707)	25

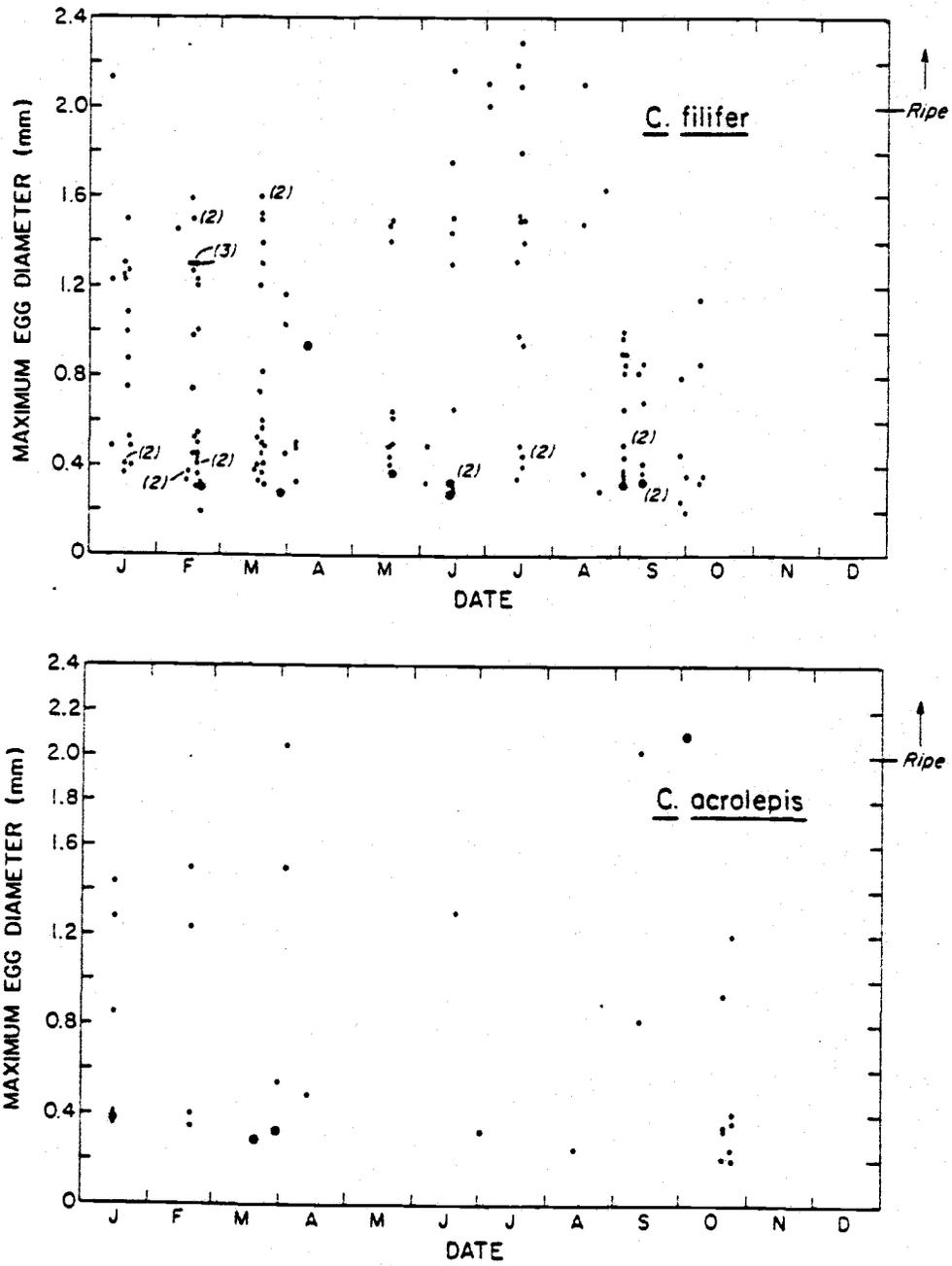


Figure 3. Occurrence of ripe females of Coryphaenoides filifer and C. acrolepis  $\geq$  500 mm TL during the year. o = spent or with atretic Stage IV eggs.

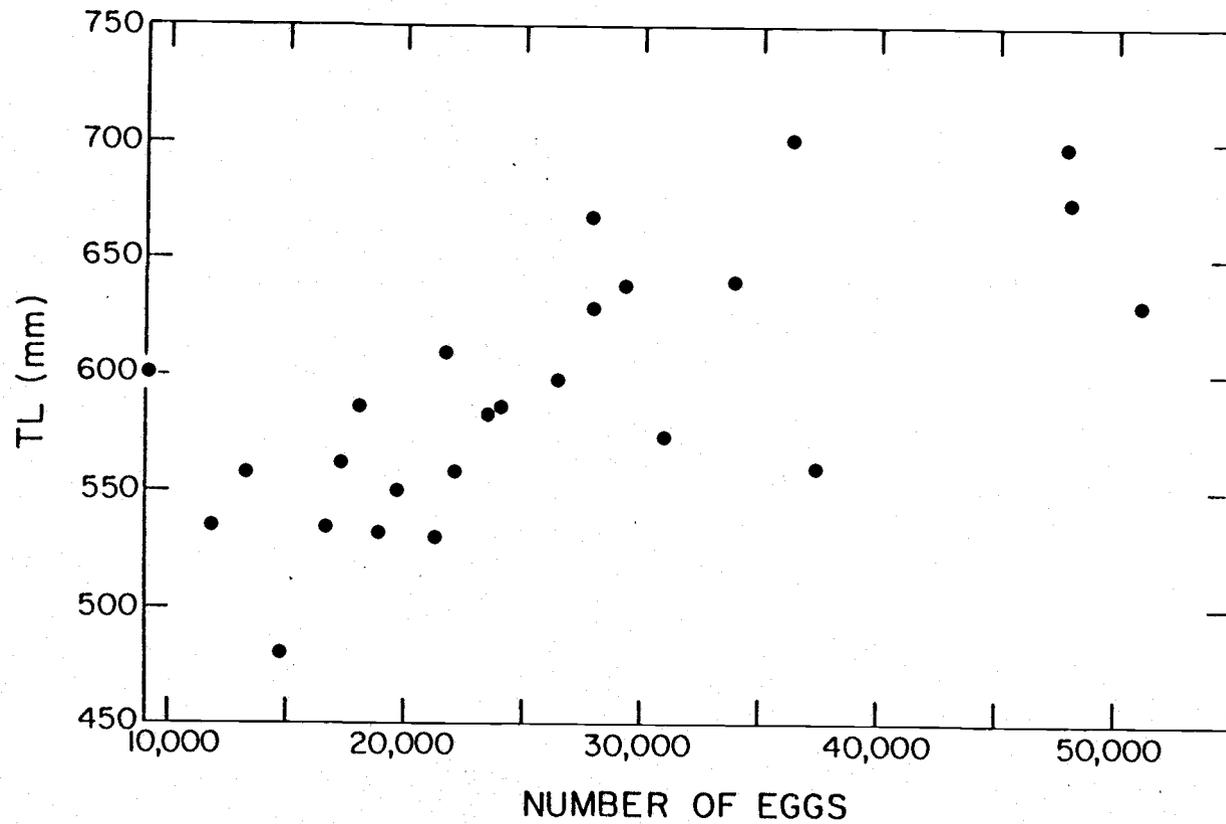


Figure 4. Fecundity vs. total length (TL) in *Coryphaenoides filifer*.

Fecundity of C. leptolepis was not estimated because no females with Stage III or Stage IV eggs were collected. Stage I and II eggs of this species are distinctly smaller than those of C. acrolepis and C. filifer (Table 3).

#### Early Life History

The available information on the morphology and distribution of Oregon macrourid larvae has been presented by Stein (1980). In summary, larvae, post-larvae and juveniles have been identified and described for three species (C. acrolepis, C. filifer, and C. leptolepis), the last tentatively, but not for any other species occurring off Oregon. No spawned eggs of any Oregon macrourid have been identified. In general, smaller C. acrolepis larvae are found higher in the water column.

Size at adoption of benthic mode of life can be estimated for the four species discussed in this paper. The largest specimens captured by midwater trawl and the smallest captured by bottom trawls are given in Table 6. Assuming that "settling" occurs at a size about equal to the average of the above two sizes (although it may well occur over a range of sizes), then C. acrolepis, C. filifer, C. armatus, and C. leptolepis become benthic at about 17.6 mm HL (100 mm TL), 20.9 mm HL (100 mm TL), 16.9 mm HL (80 mm TL), and 11.8 mm HL (50 mm TL) respectively. In C. acrolepis, and possibly in C. armatus, at least one juvenile captured in the water column is larger than the smallest individual (presumably) captured on the bottom. So few small C. filifer were captured in bottom trawls that the size at settling can only be very roughly estimated.

#### Population Structure and Distribution by Length

##### C. acrolepis

The size frequency distribution of this species may be bimodal (Fig. 5), although the small number of specimens examined (308), and the irregular sampling on the slope, where the species is most common, compromise the validity of the conclusion. Females reach 860 mm TL, but the largest male collected was only 750 mm TL (Fig. 6). Weights of males and females are very similar. For males,  $\log wt = 3.39 \log TL - 6.14$ ; for females,  $\log wt = 3.32 \log TL - 6.00$ . There may be a relationship between lengths of fishes captured and depths of capture. The smallest fishes

Table 6. Maximum lengths of juvenile macrourids captured by midwater trawls, minimum lengths of those captured by bottom trawls, and approximate lengths at settling.

<u>Species</u>	<u>Size Maxima (mm)</u>		<u>Size Minima (mm)</u>		<u>Estimated Size at Settling (mm)</u>	
	<u>HL</u>	<u>TL</u>	<u>HL</u>	<u>TL</u>	<u>HL</u>	<u>TL</u>
<u>C. acrolepis</u>	18.5	83	16.7	73	17.6	80
<u>C. armatus</u>	17.6	88.1	15.3	58 <sup>+</sup>	16.9	80
<u>C. filifer</u>	15.1	87	26.7	124	20.9	100
<u>C. leptolepis</u>	10.0	42	13.6	49	11.8	50

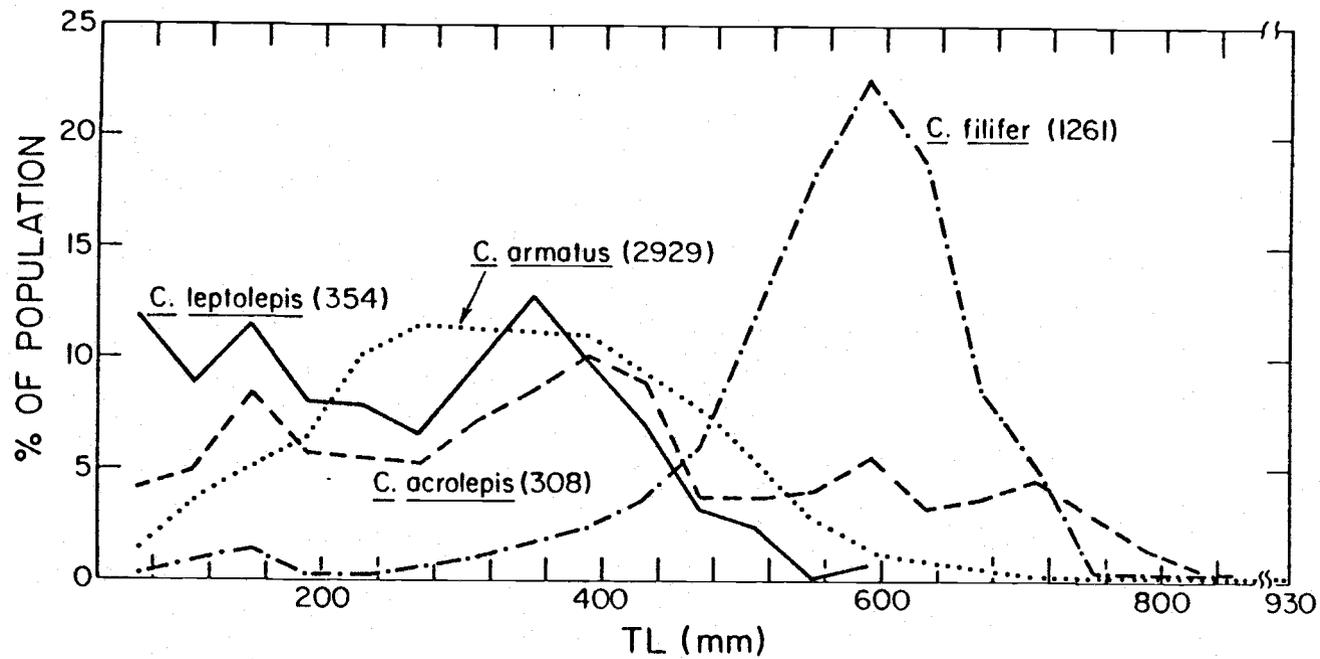


Figure 5. Total length (TL) frequency distribution of the four macrourid species studied. Numbers of individuals measured in parentheses.

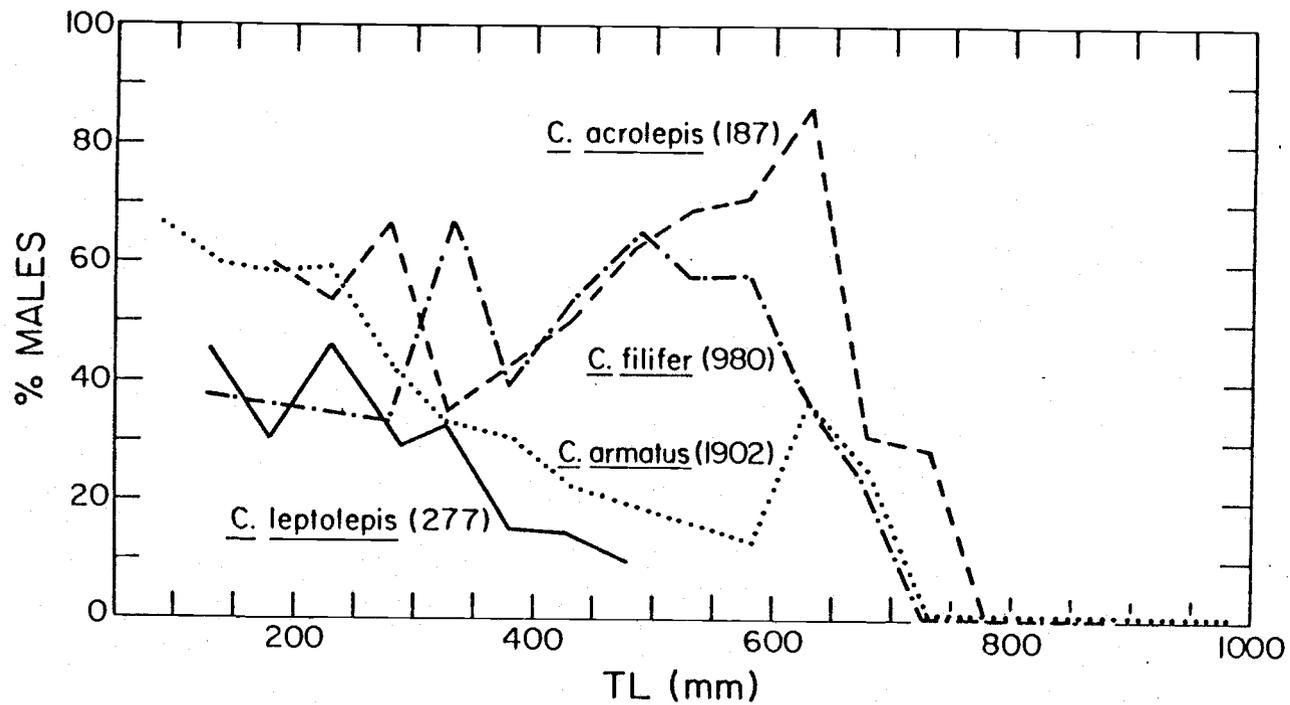


Figure 6. Percent males vs total length (TL) for the four macrourid species studied. Points representing fewer than 3 individuals omitted. Numbers of individuals captured in parentheses.

occurred at the extremes of the depth range and the largest occurred at 1600 m, although those at the shallow end of the range (possibly the most recently settled individuals) are smaller than those at the deep end (Fig. 7).

#### C. armatus

Size frequency distribution of this species is clearly unimodal, with the majority of individuals less than 330 mm TL (Fig. 5). No individual size modes were apparent, possibly because of the summation of the data. Female C. armatus reach a much greater length than do males (976 mm TL vs. 690 mm TL) (Fig. 6). At equal lengths, the sexes are approximately equal in weight. Length and weight of males are related as  $\log \text{wt} = 3.02 \log \text{TL} - 5.50$ ; for females,  $\log \text{wt} = 3.48 \log \text{TL} - 6.25$ . It is especially noteworthy that weight of the largest individuals (>800 mm TL) increases rapidly with small increases in length (Fig. 8). At large size continued growth is reflected in increased girth (i.e. weight), giving the largest individuals a much fatter appearance.

Total length clearly increases with increasing depth to 4000 m and then decreases at depths greater than 4800 m (Fig. 7). The relationship of length and depth is also obvious along the CP-1 station line, where average TL increases in deeper water to the south (Fig. 9). Because the CP-1 stations were reasonably equidistant from shore it is clear that the increase in size is related to depth. Average TL does not increase with depth along the CP-2 and CP-3 lines where depth remains relatively constant.

#### C. filifer

C. filifer has a unimodal TL frequency distribution. Average individual length is much greater than in the other species (Fig. 5). Very few small (<330 mm TL) individuals were captured by the beam trawl; they constitute only 4.2% of all captures. Females reach much greater lengths than males (860 mm TL vs. 690 mm TL) (Fig. 6). Length-weight relationships of males and females are very similar. Males:  $\log \text{wt} = 2.76 \log \text{TL} - 5.16$ ; females:  $\log \text{wt} = 2.66 \log \text{TL} - 4.94$ . Unlike C. armatus, there does not appear to be much allometric change in weight between the largest individuals and the remainder of the population (Fig. 10).

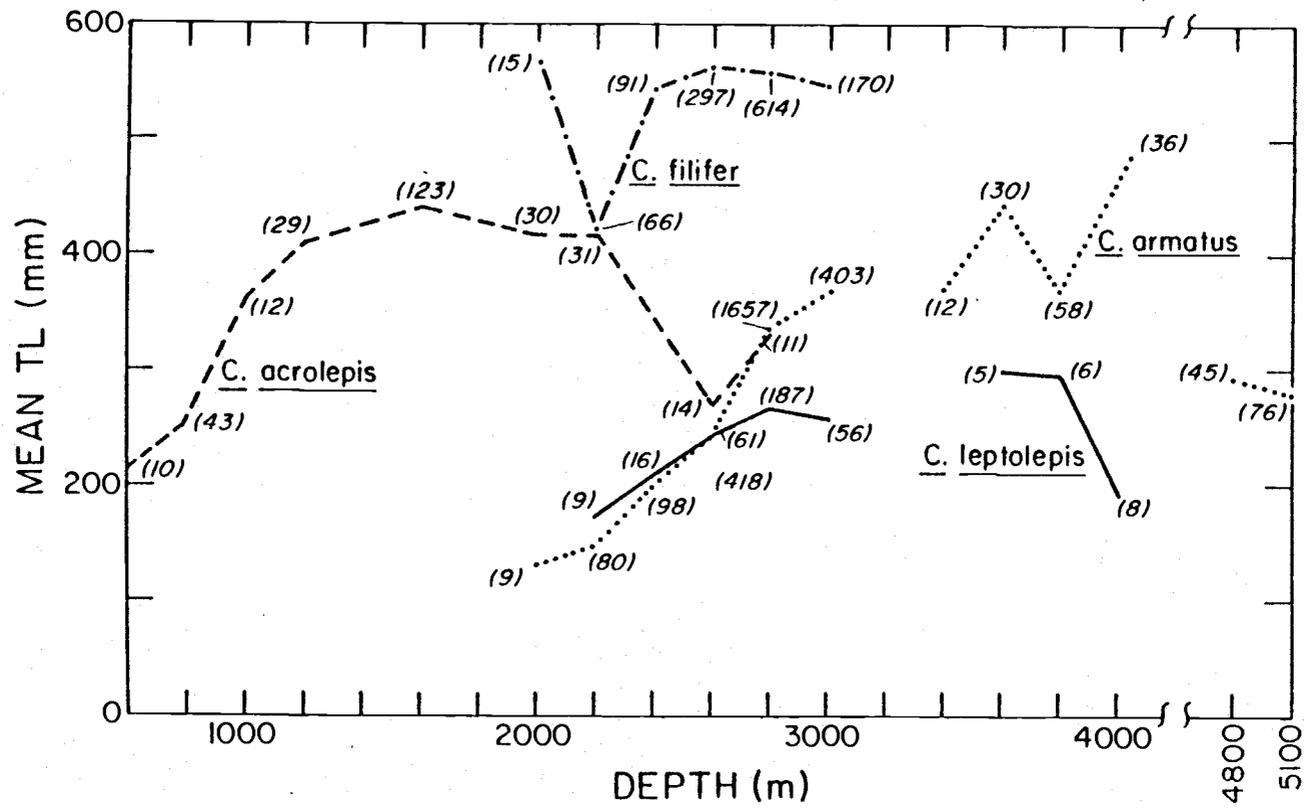


Figure 7. Mean total length (TL) vs. depth for the four macrourid species studied. Numbers of individuals represented by each point in parentheses.

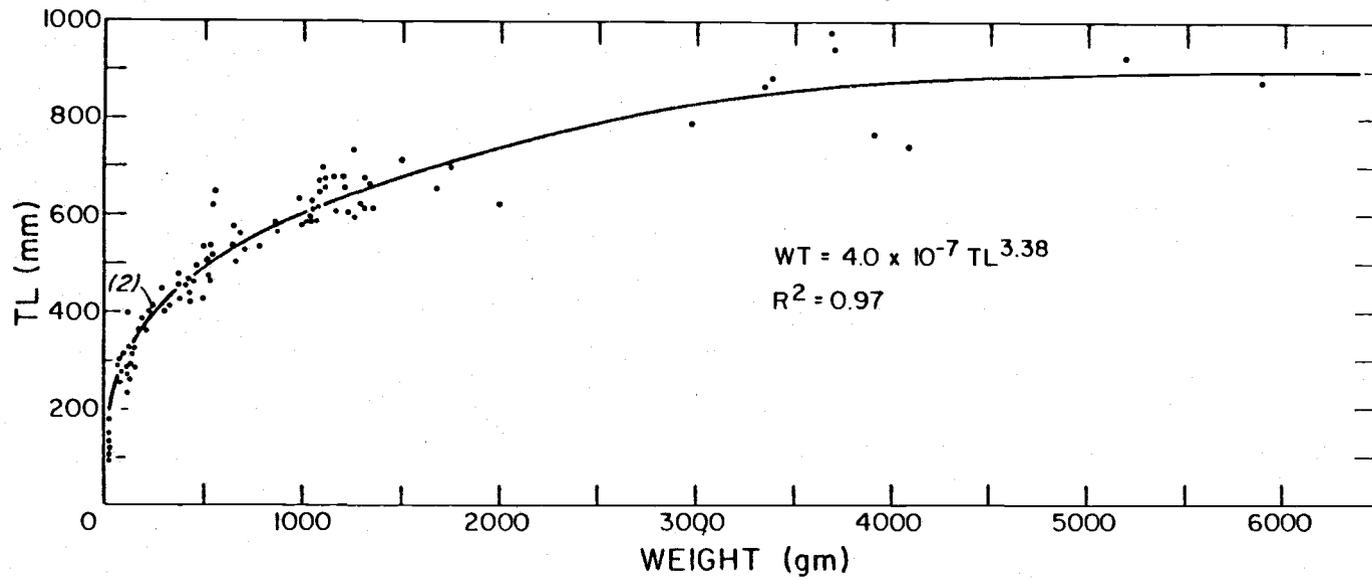


Figure 8. Total length (TL)-weight relationships of Coryphaenoides armatus.

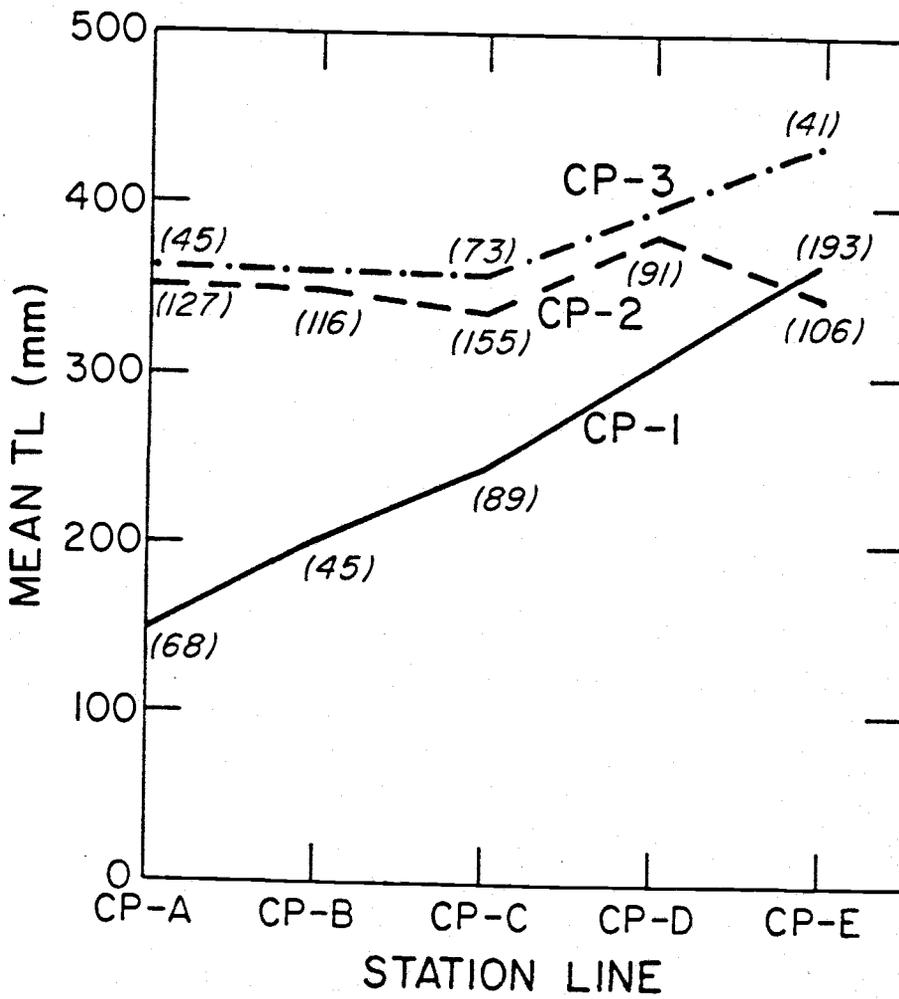


Figure 9. Mean total length (TL) vs. Cascadia Abyssal Plain stations for *Coryphaenoides armatus*. Numbers of individuals represented by each point in parentheses.

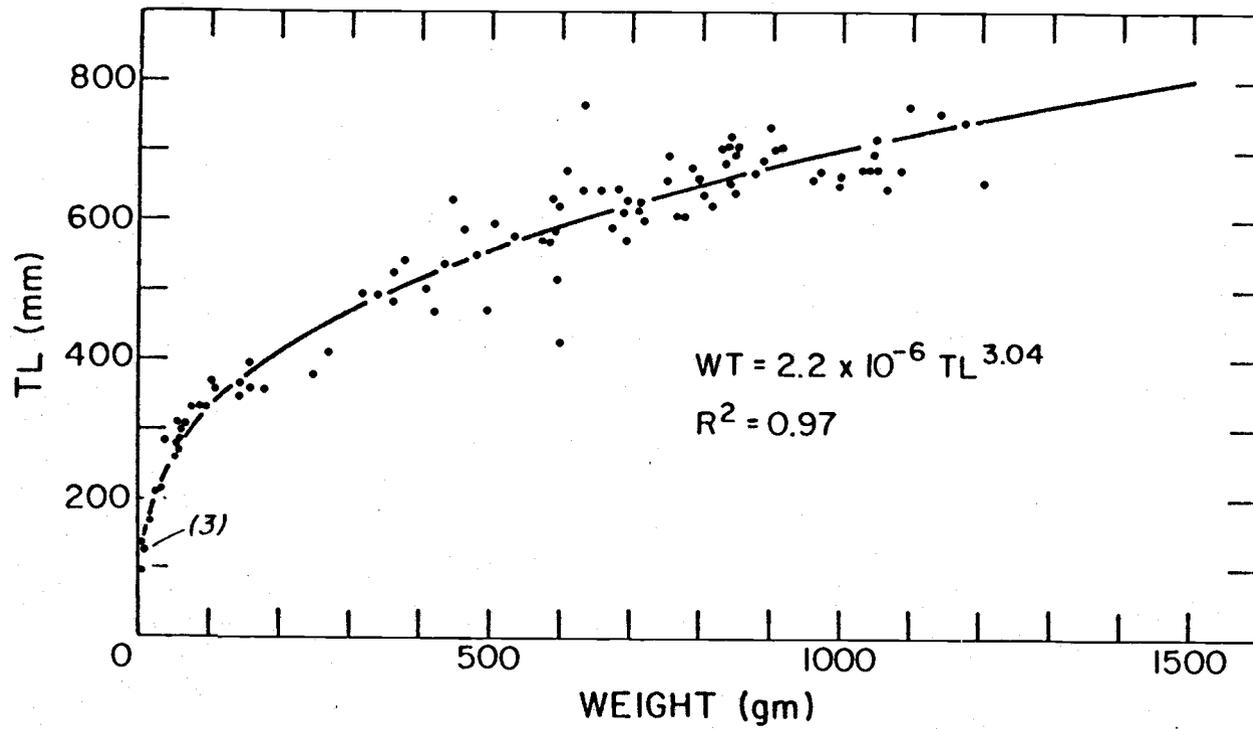


Figure 10. Total length (TL)-weight relationships for *Coryphaenoides filifer*.

There was no apparent relationship between size and depth, distance from shore, or season. Average TL was relatively constant throughout the depth range of the species (Fig. 7).

#### C. leptolepis

Length frequency of C. leptolepis is similar to that of C. acrolepis: it apparently is bimodal (Fig. 5), and the two peaks occur at approximately the same lengths as in C. acrolepis, although the maximum lengths of the two species (590 mm TL vs 830 mm TL) are quite different. There appears to be no difference in maximum length between males and females (Fig. 6), and the length-weight relationships of each sex are similar. Length-weight relationship for males is  $\log \text{ wt} = 3.23 \log \text{ TL} - 5.92$ ; for females,  $\log \text{ wt} = 3.29 \log \text{ TL} - 6.06$ . Possibly as a result of the paucity of specimens (354), no clear trends in length or weight related to environmental changes are evident. However, TL may be related to depth. A general increase in TL with depth occurred except at the deepest station (4000 m) where smaller individuals occurred (Fig. 7).

#### Population Structure and Distribution by Sex

##### C. armatus

In C. armatus, only 36% of the individuals captured were males. Although there was no evidence that either depth or season affected the sex ratio within the population, distance offshore (longitude) and TL did affect it. There was a distinct difference between sex ratios in populations from Cascadia Plain and on Tufts Plain (Chi-Square Test,  $p < 0.01$ ). The average sex ratios at longitudes less than 128°W were less than 45% males, while those at longitudes of 131°W or greater were equal or greater than 50% males. The stations farthest offshore had over 90% males (Fig. 11). Total length affects sex ratio; there was a steady decline in % males with length (Fig. 6), except at the largest sizes (>600 mm TL). Even at those lengths, fewer than 40% of individuals were males. No males longer than 730 mm TL were found.

Aggregation by sex was not evident (Fig. 12). There were few tows in which the percentage of males or females was high ( $\geq 80\%$ ), whereas the number where sex ratios were about equal to the overall population average was almost 40% of the total number of tows.

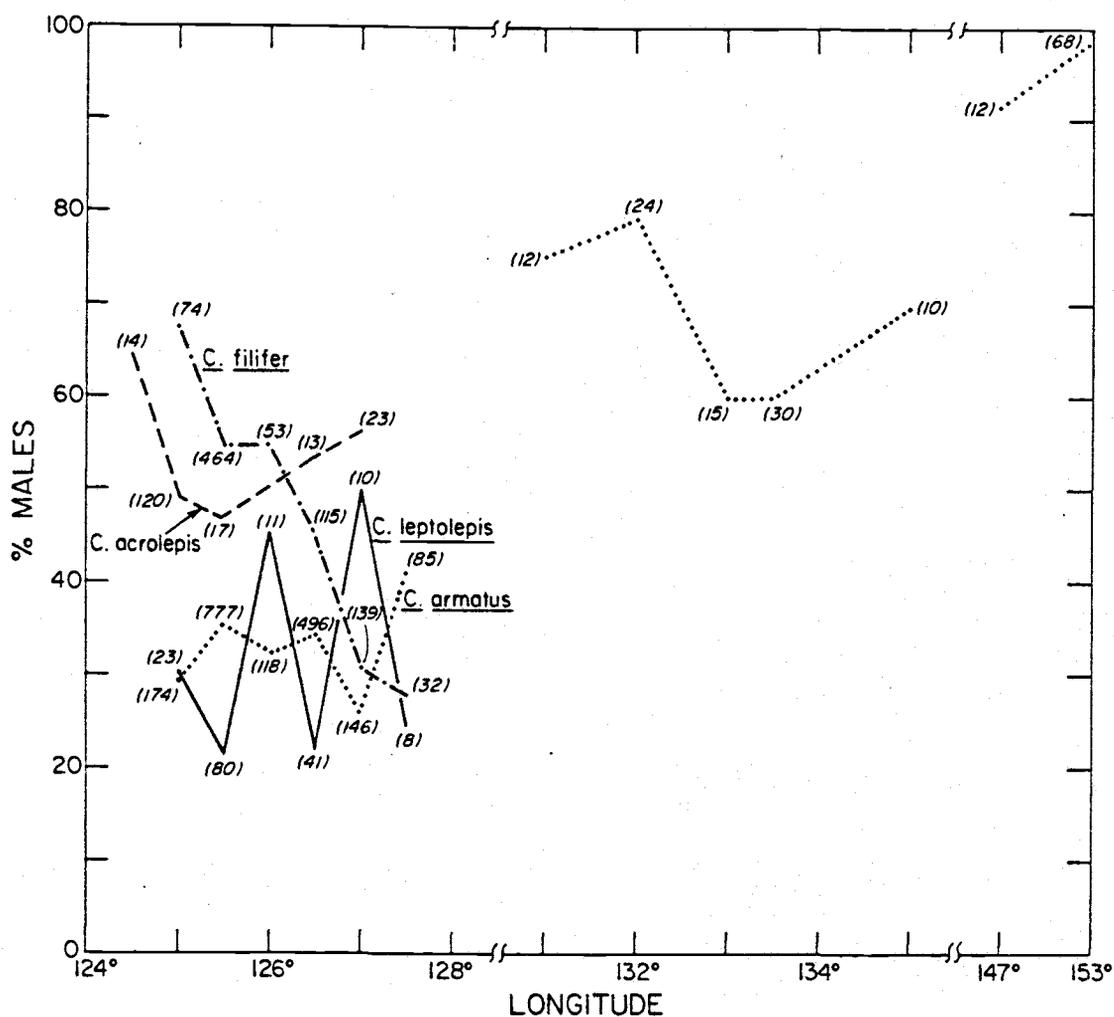


Figure 11. Percent males vs longitude for the four macrourid species studied. Number of individuals represented by each point in parentheses.

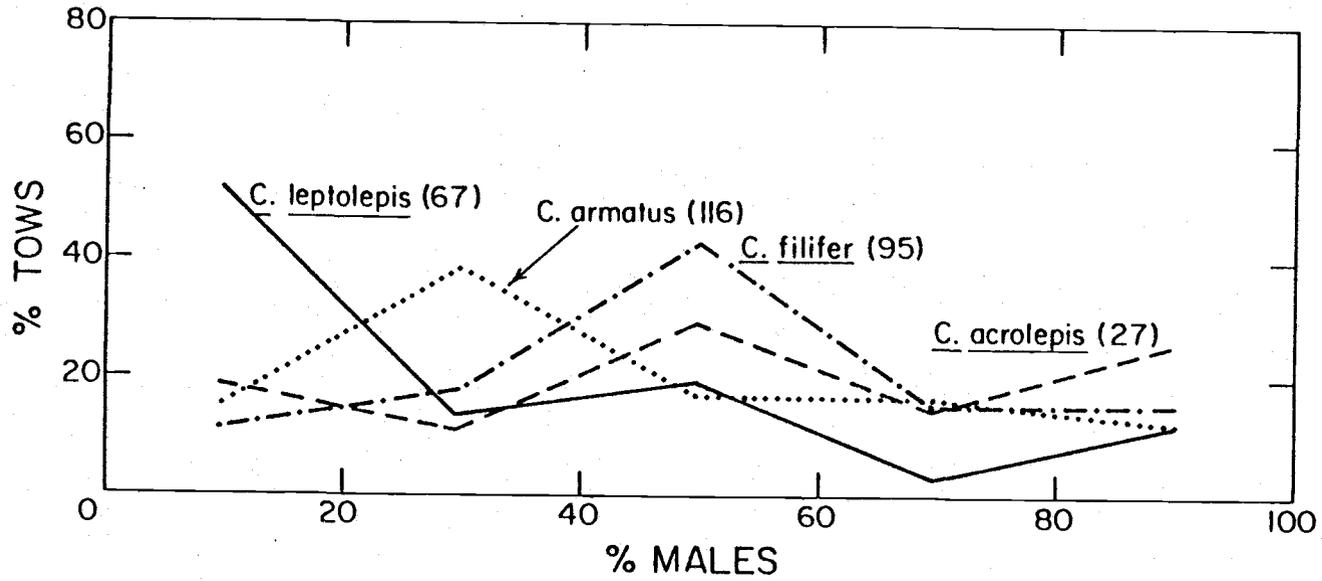


Figure 12. Percent males of each macrourid species per tow vs. occurrence in tows. Number of tows in parentheses.

C. filifer

In C. filifer, overall sex ratio was about 1:1 - quite different than that observed in C. armatus. A relationship between sex ratio and depth or season was not evident. Abundance of males clearly decreases with increasing distance from shore (longitude) (Fig. 11). Length and sex ratio are weakly related. The percentage of males remained relatively constant with increasing length until about 580 mm TL, after which it declined rapidly to 0 at about 730 mm TL (Fig. 6).

Aggregation by sex was not evident (Fig. 12). The percentage of tows in which sex ratio was about equal to that in the population was about 43%, and the percentages of tows in which males and females formed a high proportion of the catch was low.

C. leptolepis

Coryphaenoides leptolepis males were relatively rare; only 36% of the individuals captured were male, and females were more abundant at all sizes (Fig. 6). Too few specimens were collected to allow reliable analyses of sex ratio changes with environmental variables. The results of such analyses seem to show that there is no change with depth, distance from shore, or season. There is a gradual decrease in percent males with increasing TL, although the sexes apparently reach similar maximum lengths (Fig. 6).

Whether C. leptolepis aggregate by sex is unclear (Fig. 12). In over 50% of the tows, females comprised 90% of the catch, but in only 12% of the tows did males comprise 90%. However, no peak occurred (as in other species) at total percent males (36%) in the population. If sexual segregation exists, there should be few catches with high percentages of males and females, and many composed almost exclusively of males. This was not the situation. We conclude that there is no sexual segregation.

C. acrolepis

The overall sex ratio in this species was about 1:1; as in C. leptolepis, too few specimens were captured to allow firm conclusion about sex ratio. However, males were most abundant in the collections furthest inshore and offshore (Fig. 11). Unlike the other species, the

percent of males may actually increase with greater length until about 630 mm, after which it appears to decrease rapidly (Fig. 6).

Sexual segregation is not evident. The greatest percentage of tows occurs at about 50% males, which approximates the overall sex ratio in the population. The extremes (highest and lowest proportions of males within tows) however, are relatively high (Fig. 12), suggesting that more data might change the results. Sexual segregation might exist in certain areas or at some times of the year. The necessary combination of our data (because of the low number of specimens obtained) could hide or confuse the actual situation.

#### Abundances of Relatively Recently Settled Juveniles

These abundances vary among the species. Small acrolepis, armatus, and leptolepis are relatively common. Coryphaenoides acrolepis less than 90 mm TL constituted about 4.2%, armatus about 1.3%, and C. leptolepis were 11.7% of those captured. Coryphaenoides filifer, however, were rare at all small sizes; only 0.2% of those collected were shorter than 90 mm TL. These abundances are reflected in the size frequencies of the species (Fig. 5).

It may be significant that of the four species, C. filifer may be much larger (almost twice as large as C. leptolepis) at settling as the others (Table 6). This difference suggests that small C. filifer are not captured with bottom trawls because they are in the water column until a relatively large size. However, the low number of small C. filifer collected does not allow a definite hypothesis.

#### Liver Weights

Although not enough livers were examined to allow complete analysis of seasonal or reproductive hepatic cycles, the results do show distinct differences in relative liver size between large C. armatus and C. filifer.

The relationship of percent liver weight to TL in C. armatus and in filifer is positive (Fig. 13). In C. armatus, males have significantly larger livers than females (t-test,  $p \leq .001$ ). In C. armatus, unlike C. filifer, the proportion of weight represented by the liver may be quite large (up to 13.2%). In males greater than about 400 mm TL and in

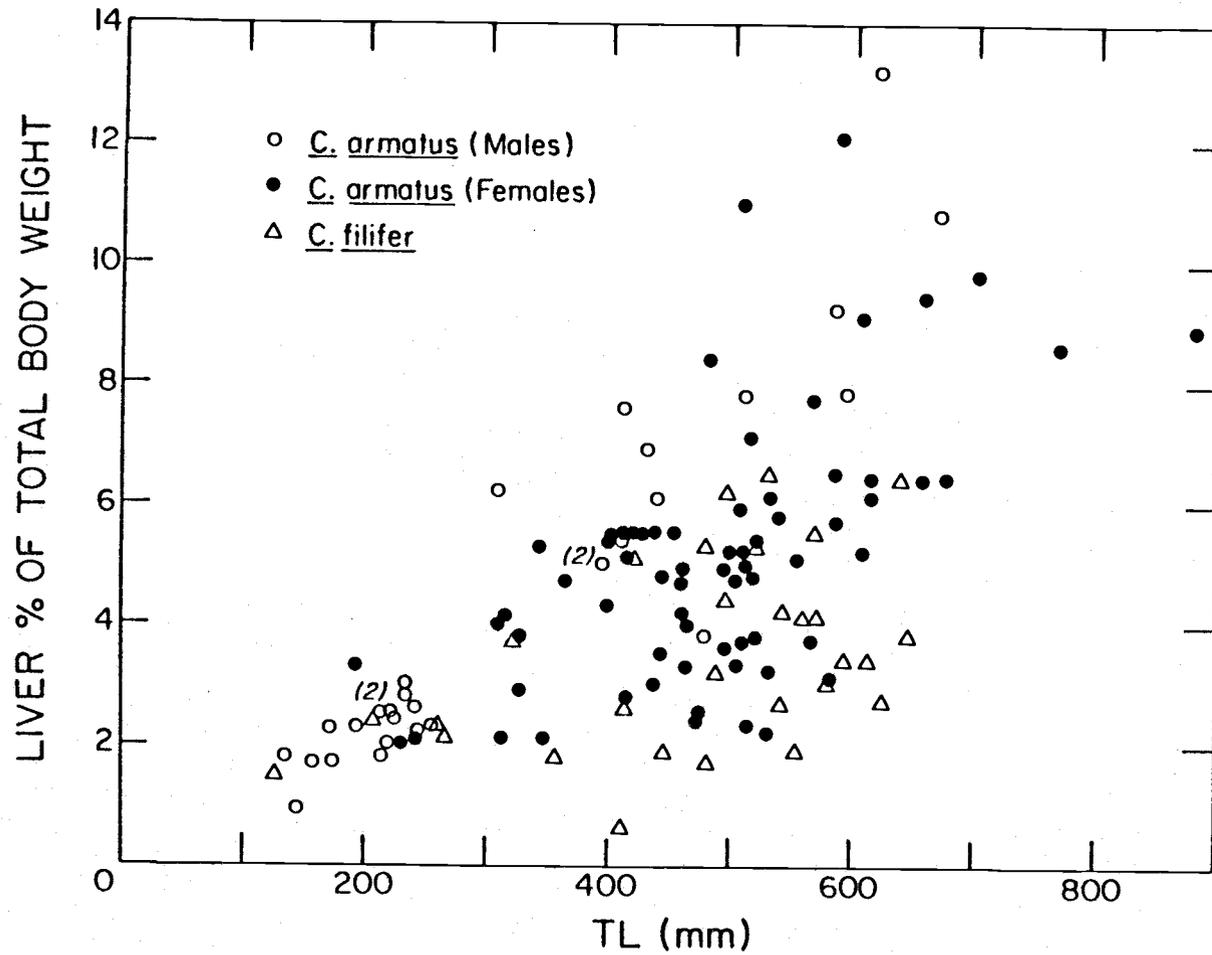


Figure 13. Relative liver weight (% of total body weight) in *Coryphaenoides armatus* and *C. filifer*.

females over 500 mm TL liver weight was often over about 6% of total body weight. All individuals above 610 mm TL had liver weights above 6% total body weight. In C. filifer, liver weight reaches a maximum of a little over 6% at about 500 mm TL and does not increase with greater length. Differences between liver weights of males and females were not analyzed.

Thus, increase in relative liver weight in C. armatus does not seem to be related to sex. Both sexes showed such increases although most high values were for females, probably because few males reach very large size. The individual with the proportionately largest liver, however, was a male. Females with large livers had ovarian eggs of Stage I or III, suggesting that liver weight is not related to the ovarian development cycle. No relationship with season is apparent: individuals with liver weights of about 9% body weight or greater were captured in February, May, June, July, and September (Fig. 14).

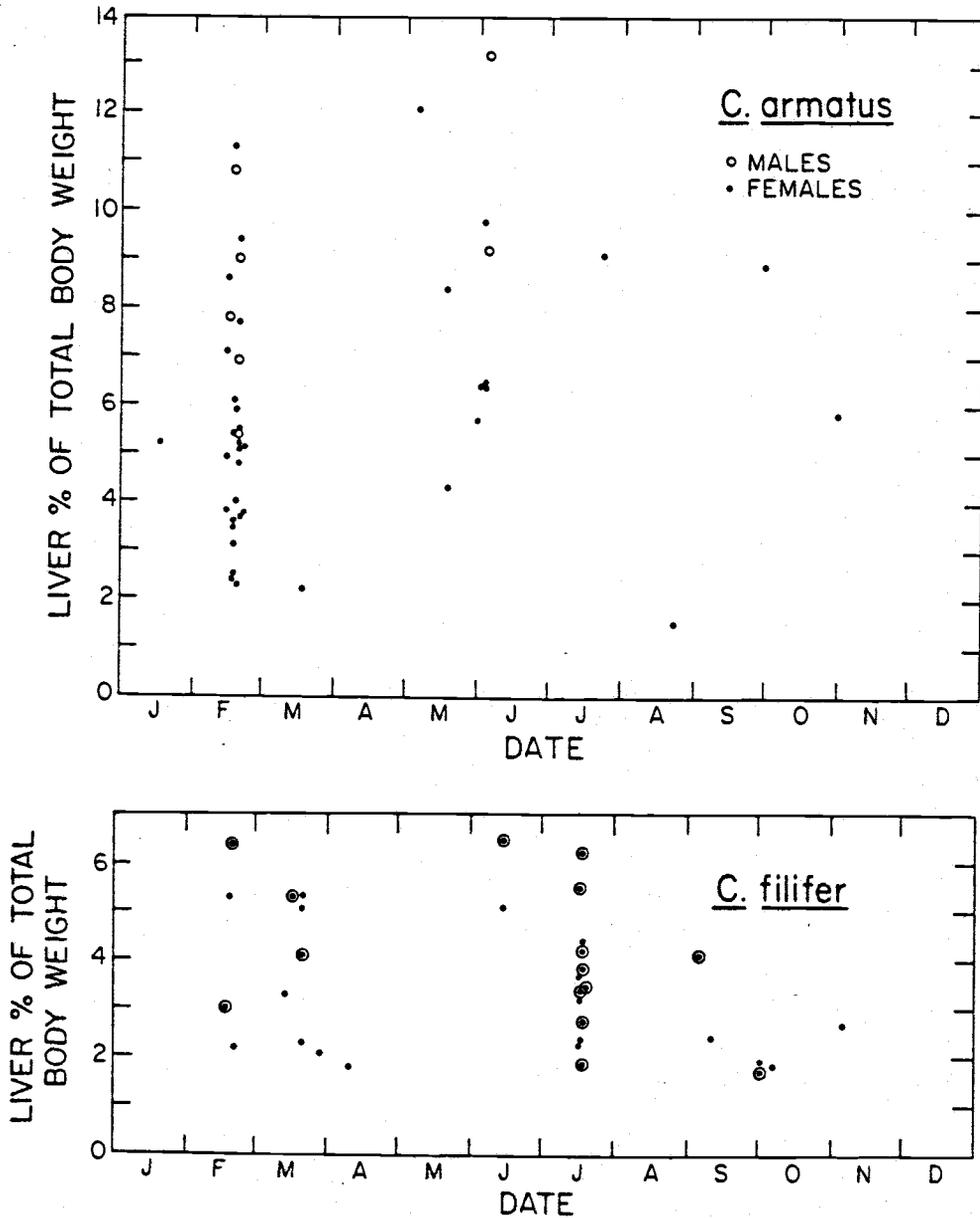


Figure 14. Relative liver weights (% of total body weight) vs. capture date in *Coryphaenoides armatus* and in *C. filifer*. ○ = *C. filifer* >500 mm TL.

## DISCUSSION

The relatively little data available on relationships of size of macrourids to depth generally concerns slope-dwelling species. In all macrourid species in which it has been examined, length is positively depth dependent (C. carapinus Goode and Bean: Haedrich and Polloni, 1976; Nezumia aequalis (Günther), Coelorhynchus coelorhynchus (Risso), Trachyrhynchus trachyrhynchus (Risso): Macpherson, 1979; T. trachyrhynchus: Ibañez, 1977; Nezumia bairdii (Goode and Bean):Wenner, 1978:275; C. armatus, C. leptolepis: Polloni, Haedrich, Rowe, and Clifford, 1979). Our results for C. armatus and C. leptolepis are similar, except for the abrupt decrease in length at the greatest depths (Fig. 7). The deep captures of both species are at about their maximum depths of occurrence (C. armatus:Haedrich, Rowe, and Polloni, 1980; C. leptolepis:Grey, 1956), suggesting that the small average size of these individuals indicates the environment is unsuitable for optimum survival and growth. Neither C. filifer nor C. acrolepis shows a clear depth related size trend (Fig. 7). However, few C. acrolepis were captured, and the depth range of C. filifer was the narrowest of all four species (ca. 1000 m).

Polloni et al. (1979) suggest that the reason for increasing size with depth is that increased foraging efficiency is required in the deep-sea due to decreases in available food. Average length of Coryphaenoides armatus is much shorter than that of C. filifer at comparable depths (Fig. 7). Average TL (500-600 mm) of C. filifer is also about the same across its benthic depth range (2000 to 3000 m), while Coryphaenoides armatus increases from about 130 mm TL to 360 mm TL over the same range. Even at the maximum the average length of C. armatus (470 mm TL, ca. 4000 m) doesn't equal that of C. filifer. Possibly individuals of C. filifer up to 480 mm TL are more pelagic than C. armatus and consequently are only available to bottom trawls at larger sizes. The relative rarity of small C. filifer tends to support this hypothesis.

Competition with C. armatus for food may be a reason for the differences in sizes of near-bottom individuals of these two species. Coryphaenoides armatus is much more abundant than C. filifer in virtually all the samples (Pearcy et al., unpublished). Pearcy and Ambler (1974) described and discussed food habits of these two species. Both species eat nekton, and there is a broad overlap in types of food items eaten. Food habits of individuals of each species of "average" length at a given depth are similar. Coryphaenoides armatus of 130-360 mm TL ate primarily (% by weight) benthic crustacea, holothurians, and cephalopods; C. filifer of 400-500 mm TL ate primarily crustaceans and holothurians.

Mouth size clearly determines sizes of prey which can be eaten (McLellan, 1977). Differences in mouth size exist between individuals of the two species at the same TL (Fig. 15). Although the slopes of the regression lines are similar, the intercepts are different at the .90 level of significance. C. filifer has a larger mouth than C. armatus, which tends to accentuate differences in size of food organisms available to these species. Thus, even though the food items eaten are of the same categories, they are probably of different average sizes. Fishes of the same lengths have different feeding habits: C. armatus of 400-500 mm TL ate cephalopods and fishes. The C. filifer, on the average larger than C. armatus feeding on similar items, might well be more efficient at foraging than the smaller C. armatus. Differences in size at time of settling (Table 6) may accentuate differences in mouth size existing at that time. Thus, C. armatus is the dominant species, small C. filifer occur in the water column where competition is reduced, and large C. filifer occur on the bottom because of reduced overlap in feeding habits with C. armatus.

Coryphaenoides acrolepis shows a somewhat different distributional pattern by size than the other species studied. Although the average size of the shallowest individuals is smallest, there is apparently a sharp decrease in average size at depths greater than 2200 m (Fig. 7). Average TL of individuals at these depths is less than at any other depths except those at 800 m or shallower. In this instance two factors may be operating. First, the shallowest individuals may be the most

recently settled. Stein (1980) supported the hypothesis that C. acrolepis has an ontogenetic migration, and showed that individuals of up to about 19 mm HL (about 104 mm TL) can be collected in the water column. Preferred depth of settling is unknown, however, Second, the smaller individuals at the deeper end of the distribution might be reflecting the same phenomenon as that apparently shown by C. armatus and C. leptolepis.

Examining all four species together, there seem to be two pairs of species by pattern of size frequency: C. armatus/C. filifer and C. acrolepis/C. leptolepis. The populations of the first pair show unimodal TL frequencies; those of the second show bimodal TL frequencies. The expected frequency distributions from fishes like these, which are (presumably) long-lived and slow growing, are unimodal, with the mode either at the "small" end of the size range or flat (non-modal). In such fishes, year classes would not appear clearly (or appear at all) in the population length frequency. The size distribution of C. armatus is similar to the expected unimodal type, with a mode of small individuals and fewer large ones. That of C. filifer is not expected. Although unimodal, the mode is one of large individuals; the small ones are almost absent. Coryphaenoides filifer postlarvae are substantially longer than pelagic juveniles of C. armatus (Stein, 1980) suggesting that small C. filifer are not available to capture by bottom trawls or occur in unsampled areas.

Net avoidance by large C. armatus could shift the length frequency curve to the left. C. armatus of sizes comparable to those of large C. filifer (which apparently are not good avoiders) seem unlikely to be better at avoiding the net than C. filifer. The problem of explaining these differences is exacerbated by the known occurrence of both C. filifer and C. armatus well off the bottom (Pearcy, 1976; Smith, White, Laver, McConnaughey, and Meador, 1979), making assumptions about adequate sampling of populations of these species difficult to defend.

In the second group, the meaning of the bimodal length frequency distributions is problematic. It may be an artifact of sampling, because neither species is well represented in the OSU samples. Possibly the

samples are too small, or the correct areas were not sampled. This is especially possible for C. acrolepis, which may be sexually segregated (Scripps Institution of Oceanography, 1975) although the data collected for this study does not indicate that such segregation occurs (but see "Results" above).

#### Population Sex Ratios

In C. acrolepis and C. filifer, the ratio of males to females in our samples was about 1:1, but in C. armatus and C. leptolepis, females predominated. These differences are difficult to explain because of the difficulties of in situ study of living rattails. Possibly males mature younger than do females of the last two species, redressing the apparent imbalance among mature individuals. Hermaphroditism is unknown in any macrourid or gadiform fish (Breder and Rosen, 1966; Marshall, 1979:459). In the species considered here there is no change in predominance of either sex at any specific size, ruling out possible protogyny and protandry. Furthermore, the ovaries and testes of females and males are clearly distinguishable (except at the smallest, least mature sizes), eliminating the possibility of functional synchronous hermaphroditism. Without information on age, rates of mortality, and information on actual spawning habits, determination of the significance of sex ratio differences is very difficult.

Based upon similarities in sex ratios and geographic occurrence, the species can also be divided into two pairs: armatus/leptolepis, and acrolepis/filifer. The first pair have overall sex ratios of fewer than 50% males; the decline in proportion of males with increasing size is more or less steady; both species occur on Tufts Abyssal Plain (although leptolepis is not abundant) and ripe females of neither species have been collected. In the second species pair there are approximately equal numbers of males and females; the decline in % males per size category is abrupt, occurring at greater than 650 mm TL; neither species occurs on Tufts Plain; and ripe females of both species were collected.

Sex ratio varied little with season or with depth. C. armatus and C. filifer sex ratios are affected by distance offshore (taken as longi-

tude) (Fig. 11). The percentage of the armatus population which is male is very high west of 131° longitude; there is no overlap in sex ratios between the inshore areas (Cascadia Plain) and the offshore ones (Tufts Plain). Coryphaenoides filifer shows the opposite pattern; % males decreases quite steadily from East to West. The amount of change is considerable (from 67% males to 28% males) and the rate of change is rapid (Fig. 11).

No firm evidence for schooling or aggregation by sex was found. Coryphaenoides acrolepis was the only species for which there was a suggestion of sexual segregation. Rosenblatt and Matsui (Scripps Institution of Oceanography, 1975) found that in C. acrolepis off southern California, there was a clear difference between males and females in habitats. This segregation breaks down during spawning. We collected too few C. acrolepis to allow testing this by removing tows made during the times when we collected spawning or ripe females. Such removal (if there were enough tows remaining) would show if segregation occurred at other times of the year. In any event, the continental slope off Oregon is very rocky and uneven. Many areas (perhaps most of the slope area) cannot be sampled by trawling. If males and females are separated, except at the two spawning periods, some other sampling methods must be used to obtain specimens from presently untrawlable areas.

#### Size at Settling, Food Habits, and Competition

Of the four species considered here, the region of greatest abundance of one (C. acrolepis) does not overlap much the regions of abundance of the other three species (i.e. the continental slope vs. the abyssal plain). Consequently, for purposes of discussing the significance of settling size and time to interspecific ecological relationships it will be omitted. The other three species differ from each other in either head length, total length, or both. Coryphaenoides leptolepis is apparently the smallest at time of settling; C. armatus is intermediate, and C. filifer is the largest. Differences in size at settling may be a means of minimizing competition among the three species. The species most closely associated with the bottom (C. leptolepis) is smallest at settling. All the other species have been collected well

off the bottom as adults (C. acrolepis: Iwamoto and Stein, 1974; C. armatus, Smith et al., 1979; C. filifer, Percy, 1976). Percy and Ambler (1974) suggested that C. leptolepis is better suited for benthic life than its sympatric congeners by having a smaller swimbladder. No information is available about time of settling.

In three of these macrourids, size clearly affects feeding habits (Percy and Ambler, 1974). No information is available about food preferences of small juveniles (armatus, leptolepis >100 mm TL or filifer <200 mm TL) of these species, although they probably utilize microhabitats rather than being wide-ranging foragers as are adults. If we assume a continuous trend of changing food habits with size, then small juveniles have food habits differing from those of adults. Many adult food items (fishes, in particular) are not likely to be available to small rattails. As suggested above, C. filifer post-larvae and juveniles probably avoid competition by remaining pelagic longer. Coryphaenoides armatus and C. leptolepis have different food habits as adults, but as juveniles they generally eat the same kinds of prey (Percy and Ambler, 1974). Food is generally considered a limiting resource in the deep-sea (Percy and Ambler, 1974; Rex, 1976; Smith, 1978; and many others). Isaacs (1969) and Isaacs and Schwartzlose (1975) suggested that "large organic falls" such as dead whales could play an important role in the abyssal food supply. Haedrich and Rowe (1977) supported this idea. Such additional food sources are probably available only to adult macrourids, which possess the motility and large mouths necessary to find and eat such foods. Small juvenile macrourids seem unlikely to find such items or compete with the other organisms feeding on them. Thus, the individuals newly recruited to the benthic population face the more "traditional" limited food resources. Differences in mouth size might reduce competition for food by causing size differentials in prey items eaten. Mouth sizes of the macrourids considered here are different (Fig. 15). Such size differences exist throughout life, although they are relatively larger in smaller individuals. Thus, even though the kinds of prey eaten by sympatric C. armatus and C. filifer are similar, the sizes may be quite different. No information is available concerning such differences.

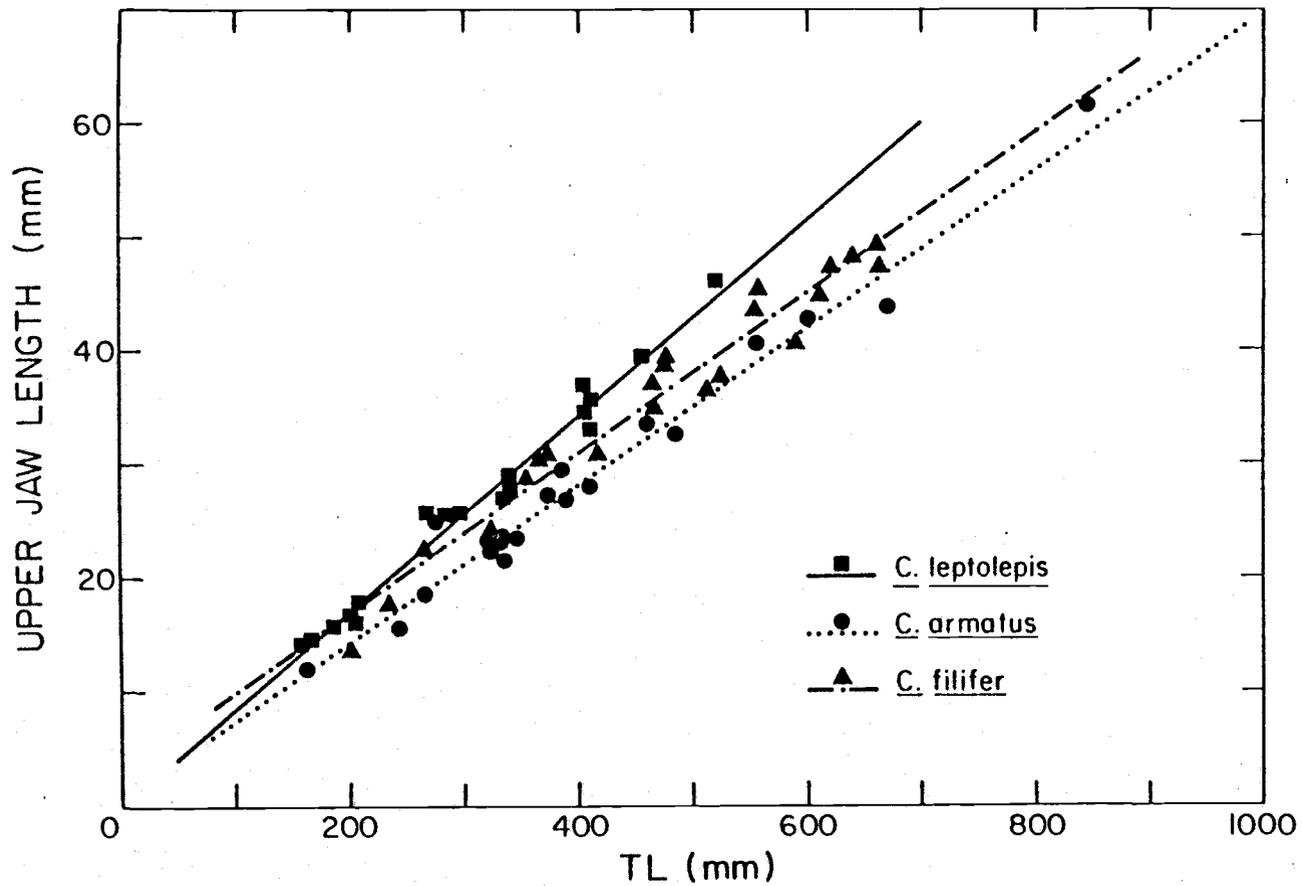


Figure 15. Length of upper jaw vs. total length (TL) for Coryphaenoides armatus, C. filifer, and C. leptolepis.

### Liver Weights

In C. armatus the liver becomes relatively much larger in the largest individuals. This phenomenon occurs in both males and females, and has not been reported previously. It is known to occur in cods (Savvatimskii, 1969:62), in at least two macrourid species, Coryphaenoides rupestris Gunnerus and Macrurus berglax Lacépede (Savvatimskii, 1969:63,65), in skates (Bone and Roberts, 1969) and in Bathysaurus (Marshall and Merrett, 1977). In C. rupestris, the males have relatively heavier livers (as in C. armatus) and liver weight is apparently cyclic (Savvatimskii, op. cit.), related to food abundance.

Too few large C. armatus and too few C. filifer were examined to provide evidence either supporting or denying the existence of hepatic cycles in abyssal fishes. However, in the latter species at least, a broad range of relative liver sizes exists at any time of year (Fig. 14) and that the largest livers occurred in February, June, and July. These months do seem to correspond with known spawning times, but as the samples represent so few fishes, caution is required in interpretation. In C. armatus, there is apparently no trend of liver size with season or reproductive state.

Possible functions of such relatively large livers are three. The liver may store energy for spawning (Savvatimskii, 1969:62; Hureau, 1970); it may serve as a repository for energy to be used in overwintering or in times of food scarcity (Smith, 1978), and it may serve as a buoyancy mechanism (Marshall and Merrett, 1977). In C. armatus, because increased liver size is not limited to one sex and in females does not seem to be correlated with either egg stage or time of year, the liver probably acts as a buoyancy device. With growth, individuals of C. armatus become much more robust. Rather than increasing in length, they increase in girth. The resulting appearance change (very large individuals look quite different from small ones) probably accounts for at least some of the synonymous names (there are at least eight) given the species. Because food abundance in the deep-sea is probably constant, it seems unnecessary for fish to store the very large amounts of energy represented by a greatly enlarged liver. Many authors have suggested that large

abyssal predators, such as C. armatus, are dependent for food on carcasses of large animals sinking from above (Isaacs, 1969; Curtis, 1971; Dayton and Hessler, 1972; Clarke and Merrett, 1972) or on pelagic feeding (Haedrich and Henderson, 1974; Okamura, 1970b). Thus, food supplies could be erratic, yet small C. armatus and large C. filifer do not have enlarged livers. Smith (1978) computed that the stored glycogen and lipid content in C. armatus could sustain the fish for 186 days. At least two of the specimens used in his analysis were large enough (535 mm, 685 mm TL ) to have greatly enlarged livers. He also noted that "respiration per g wet weight decreased with increasing size." Such a change could make it possible to store more food and thus increase liver size if foraging efficiency increases more rapidly with size than do metabolic requirements. Indeed, the large size of these particular individuals suggests that food may not be as limiting to growth as it is in smaller fish. Therefore, it seems most likely that as C. armatus grow, the swimbladder does not grow proportionately, resulting in little increase in swimbladder lift. The increase in fat content resulting from disproportionate liver growth may help to make up the difference. Furthermore, if, as the results of Haedrich and Henderson (1974) suggest, the largest C. armatus are more pelagic, the ability to migrate far off the bottom without having to compensate for decreased external pressure could be an advantage. Such changes occur in other, unrelated deep-sea benthic fishes (see above).

#### Growth

Growth rates of macrourids, especially abyssal macrourids, are very difficult to determine. At present, no evidence relates any of the common measures used for aging fishes (otoliths, vertebral growth rings, scale annuli) to consistently occurring natural cycles at abyssal depths. Several investigators have shown that scales can be used for aging macrourid species of the continental slope. Motais (1960) and Ibañez (1977) were both able to correlate year classes occurring in captured T. trachyrhynchus with scale annuli. Soviet investigators studying other slope macrourid species have consistently assumed that annular scale rings represent annual growth in North Pacific species (C. acrolepis, C.

pectoralis, C. cinereus, C. angustifrons: Kulikova, 1957; C. pectoralis: Novikov, 1970) and in North Atlantic species (M. rupestris, M. berglax: Savvatimskii, 1971a) without supplying supporting evidence. Using otolith structure, other investigators have drawn similar conclusions about different slope species (Nezumia sclerorhynchus: Rannou, 1976; M. rupestris: Savvatimskii, 1971a). Rannou (op. cit.) was able to relate size classes of captured fishes to otolith rings. Brothers et al. (1976), studying otoliths of C. acrolepis, found what they interpreted as "apparently daily" growth rings in what they thought were 10 to 11 year old fish. The method used to determine age was not explained. Thus, at least in some bathyal macrourid species, age can be determined by examination of scale structure and/or otoliths. However, all these species occur at depths where there are significant seasonal effects (Rex, 1976). Some of these species make migrations up and down the continental slope (C. pectoralis: Novikov, 1970; M. rupestris: Savvatimskii, 1969; Pechenik and Troyanovskii, 1970). Consequently, mechanisms which account for the presence of annual growth cycles can easily be shown. This is not true for abyssal fishes.

In the absence of data showing the existence of consistent seasonal or annual changes in the physical environment at abyssal depths, we believe that the apparent growth checks represented by otolith, scale, and vertebral rings cannot presently be related to any regularly occurring environmental phenomenon. Furthermore, the apparent occurrence of more than one or of prolonged spawning periods in C. filifer and C. acrolepis suggests that such growth "indicators" may not be annual at all. Guennegan and Rannou (1979) suggested that the existence of semi-diurnal tidal currents to at least 4000 m depth provides an environmental cue for fish behavior. Such cycles could (in theory, at least) supply necessary cues for daily growth rings (apparently shown in C. acrolepis by Brothers et al., 1976), but do not explain annual rings. Macrourids display cyclic physiological phenomena, which are represented by the various growth rings, as suggested by Rannou and Thiriote-Quievreux (1975) and Hureau, Geistdoerfer and Rannou (1979). However, these need not represent regularly occurring temporal events. As stated above, a

number of investigators have postulated the dependence of macrourids on large carcasses for food. If this is true, growth might be irregular, based upon "feast or famine" food availability events. Such growth has been suggested in bathypelagic fishes by Childress, Taylor, Cailliet and Price (1980). Because of these problems, we have made no attempt to age macrourids or describe any growth or mortality curves.

In general, as with most deep-sea fishes, macrourids are considered to be relatively slow growing and long-lived - obvious result in an environment where metabolic rates are much slower than at shallower depths (Grassle, 1977; Smith and Hessler, 1974; Smith, 1978). Estimates of growth of different slope species vary widely between species. Estimated ages of some species are long: M. berglax, 25 years; M. rupestris, 27 years (Savvatimskii, 1971a). Those of others living at comparable depths are much shorter: T. trachyrhynchus, 7 years (Motais, 1960); C. acrolepis, more than 6 years; C. pectoralis, 8 years (Kulikova, 1957). In recent review, Gordon (1979a) has discussed ages and aging of macrourids and some apparent discrepancies in results reported by different investigators. Perhaps the differences between these species represent real, but unrecognized problems, in the interpretation of evidence of cyclic growth.

## SUMMARY

- 1) Four species of macrourine macrourids were studied: Coryphaenoides acrolepis, C. armatus, C. filifer, and C. leptolepis.
- 2) Ripe and spent females of C. acrolepis and C. filifer were collected; both species apparently spawn semi-annually. Neither ripe nor spent females of C. armatus nor C. leptolepis were collected. Estimated fecundities were relatively high - 26,000 to 2.5 million eggs/female, depending on species and size of female.
- 3) Size at settling was estimated for all four species. Differences in size at recruitment to the benthic population, in conjunction with differences in relative size of mouth, may serve to minimize competition for food.
- 4) Size frequency distributions differed between species in both mode and form. C. armatus and C. filifer populations were unimodal, although the mode in the former occurred at a much smaller size. C. acrolepis and C. leptolepis had similar bimodal frequency distributions. In C. armatus and C. leptolepis, average size increased with depth, but did not clearly do so in the other species. Size was not related to distance offshore or season. In all species females reached larger size than males, but length weight relationships were similar in both sexes.
- 5) Sex ratios in the different species were different. In C. armatus and C. leptolepis, females were much more abundant, although the proportion of males increased with distance offshore. In C. acrolepis and C. filifer numbers of males and females were about equal, and their proportions were unrelated to depth, distance offshore, season, etc. There is no evidence for schooling by size or by sex except in C. acrolepis, which may be sexually segregated except in spawning periods.
- 6) The liver probably serves as a buoyancy mechanism in C. armatus. Large individuals (>500 mm TL) of this species may have livers which constitute up to about 13% of total body weight. Occurrence of such enlarged livers is not related to sex or season.

## ACKNOWLEDGMENTS

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## TABLES

1. Number of trawls which captured macrourids, by depth and month.
2. Number of ovary pairs examined, by species, including number in which eggs were measured and number of ovary pairs weighed to compute gonadal indices.
3. Size ranges of eggs at each developmental stage collected, for Coryphaenoides acrolepis, C. armatus, C. filifer, and C. leptolepis.
4. Means and ranges of gonadosomatic indices (G.I.) and number of specimens examined for all three species (C. acrolepis, C. filifer, and C. armatus) from which ripe or ripening eggs were collected.
5. Fecundities, total lengths, and number of specimens examined of Coryphaenoides acrolepis, C. armatus, and C. filifer.
6. Maximum lengths of juvenile macrourids captured by midwater trawls, minimum lengths of those captured by bottom trawls, and approximate lengths at settling.

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V. Fecundity, Egg Size, and Phylogenetic  
Position in Deep-Sea Benthic Fishes

David L. Stein

ABSTRACT

Benthic fishes living at depths below 2000 meters form a group of different phylogenetic composition from deep-sea pelagic fishes. The dominant families, and the group as a whole, are more advanced in the former than in the latter. The benthic fishes may themselves be divided into an "ancient deep-water" group and a "secondarily deep-water" group, based on the kinds of adaptations present, distributions, and evolutionary history.

The benthic fishes also form two groups based on fecundity and egg size. The first, with high relative fecundity and small eggs, is composed almost exclusively of ancient deep-water fishes (phylogenetically "lower" and "middle"). The second, with low relative fecundity and large eggs, is primarily composed of secondarily deep-water fishes (phylogenetically "middle" and "advanced"). The reproductive adaptations of the second group, maximizing offspring survival, apparently allowed the radiation of some shallow-water fishes into deep water.

## INTRODUCTION

Reproductive strategies of deep-sea fishes have been of interest to biologists at least since Murray and Hjort (1912). Despite possession of many more specimens and much more information about these animals, we still know comparatively little about their reproduction. In 1964, Mead, Bertelsen, and Cohen suggested that "...deep-sea fish...tend toward... two alternatives: the production of many small eggs with development in productive surface waters, or the production of few but large eggs which hatch into advanced young which develop in the deep sea." The purpose of this paper is first, to evaluate this hypothesis by using additional data now available about reproduction in abyssal benthic fishes, and secondly, to discuss the implications of the results of the evaluation concerning the evolution of deep-sea fishes as reflected by their phylogenetic relationships.

## DISCUSSION

The phylogenetic composition of the deep-sea pelagic and benthic fish faunas has been discussed by Andriashev (1953), Marshall (1966, 1979:33) and others. Most of the mesopelagic, bathypelagic, and abyssopelagic fish families are "lower" fishes, primarily in the superorders of Elopomorpha and Protacanthopterygii of Greenwood, Rosen, Weitzman, and Myers (1966). The exceptions are relatively few: some beryciforms, zeiforms, lampridiforms, ceratioids and other scattered representatives of various acanthopterygian and paracanthopterygian groups (Marshall, 1966, 1979; Parin, 1968). Certainly, in numbers of species, the stomiatoid, myctophoid, and argentinoid suborders of the Order Salmoniformes are more abundant than the other groups, either singly or combined (Marshall, 1966). The composition of the abyssal benthic fish fauna is different. It is dominated numerically and possibly in species number by the Macrouridae, a gadiform ("paracanthopterygian") family (Marshall, 1966; Briggs, 1974). Although there are many families of deep-sea benthic eels, most seem to be composed of relatively few species of low abundance. When the remaining deep-sea benthic fish families (aphyonids, brotulids, liparidids, zoarcids, plus miscellaneous others) are added to the macrourids, it is clear that the group is different, phylogenetically more "advanced" one from that which dominates the pelagic zone.

Andriashev (1953) divided the deep-sea fishes into two groups based upon morphology, distribution, and biology: "ancient deep-water" and "secondarily deep-water" forms. He proposed that the ancient forms are lower phylogenetic groups of teleosts, which evolved early into the deep-sea and have become highly specialized to life at great depths by possession of unique adaptations (bioluminescent organs, eye modifications, etc.). The secondarily deep-water fishes are from higher phylogenetic groups which evolved later, consequently moved into deep-water long after the ancient forms did so, and have not become nearly as specialized for deep-water life. These fishes usually belong to families with shallow water representatives. Among benthic fishes,

ancient deep-water families include the Alepocephalidae, Brotulidae, Halosauridae, Bathypteroidae, Bathysauridae, Ipnopidae, Macrouridae, Moridae, and Notacanthidae. Secondarily deep-water forms include the Cottidae (sensu lato), Liparididae, and Zoarcidae.

Only a few teleostean benthic fish families have representatives regularly occurring below 2000 meters. These include the Alepocephalidae, Bathypteroidae, Ipnopidae, Bathysauridae, Simenchelyidae, Synphobranchidae, Halosauridae, Notacanthidae, Lipogenyidae, Moridae, Macrouridae, Zoarcidae, Aphyonidae, Brotulidae, Cottidae, Liparididae, and Ogcocephalidae (Grey, 1956; Nielsen, 1969).

If the known fecundities and egg sizes of the deep benthic species of these families are graphed, omitting viviparous species (the majority of the Aphyonidae) which might be expected to have low fecundity, there are two groups of different phylogenetic composition (Fig. 1, Table 1). Although weight specific fecundity would be a better way to examine this relationship, such data is not available for most of these fishes. Length specific fecundity is not a good reflection of reproductive mode because differences in body shape (eels vs. liparidids, for instance) make direct comparisons difficult. Despite these difficulties, small fishes with hundreds of eggs, and larger fishes with thousands of eggs, can be considered to have high relative fecundity; similar fishes with fecundities order(s) of magnitude less thus have low relative fecundities. An egg size-fecundity index can be computed by multiplying mean diameter of ripe eggs by mean number of ripe eggs for each species. This index is a measure of reproductive effort which tends to reduce the extreme values. A Mann-Whitney U test (Tate and Clelland, 1957) showed the two groups were significantly different ( $P \geq .005$ ). There is a "low relative fecundity-large egg" group (Group I) which consists of the alepocephalids, cottids, liparidids, and zoarcids. There is also a "high relative fecundity-small egg" group (Group II) composed of notacanthiforms, anguilloids, macrourids, morids, alepocephalids, and myctophoids. The only family which consistently appears in both groups is the Alepocephalidae. From a phylogenetic point of view, "lower" and "middle" fishes appear in both groups, but with a single exception (Paraliparis

Table 1. Mean fecundities, egg diameters, group, and source of information for species plotted in Figure 1. Number following species name is the number in Figure 1.

Families and Species	Mean Fecundity	Mean Egg Diameter (mm)	Group	Source of Information
<b>Alepocephalidae</b>				
<u>Alepocephalus agassizi</u> 1	9150	2.8	II	D. Markle, pers. comm.
<u>rostrata</u> 2	3250	4.15	II	Golovan & Pakhorukov, 1980
<u>Rinoctes nasutus</u> 3	20	4.5	I	D. Markle, pers. comm.
<u>Bathytroctes</u> sp. 30	488	2.8	II	Mead, Bertelsen & Cohen, 1964
<u>Leptoderma macrops</u> 31	24	3.0	I	Vaillant, 1888
<u>Narcetes stomias</u> 32	1790	4.15	II	Golovan & Pakhorukov, 1979
<b>Bathysauridae</b>				
<u>Bathysaurus ferox</u> 4	40152	1.25	II	Wenner, 1978
<b>Chlorophthalmidae</b>				
<u>Bathytrophlops sewelli</u> 5	6000	1.0	II	Merrett, 1980
<b>Halosauridae</b>				
<u>Halosauropsis macrochir</u> 6	20922	1.15	II	Musick, Wenner & Sedberry, 1975
<b>Ipnopidae</b>				
<u>Bathymicrops regis</u> 7	520	0.5	II	Nielsen, 1966
<u>Ipnops agassizi</u> 8	170	0.5	II	Nielsen, 1966
<u>meadi</u> 9	600	0.7	II	Nielsen, 1966
<b>Liparididae</b>				
<u>Acantholiparis opercularis</u> 10	3	4.35	I	Stein, 1980a
<u>Careproctus kermadecensis</u> 11	34	8.3	I	Nielsen, 1964
<u>longifilis</u> 12	16	6.7	I	Stein, 1980a
<u>microstomus</u> 13	15	7.3	I	Stein, 1980a
<u>oregonensis</u> 14	8	4.9	I	Stein, 1980a
<u>ovigerum</u> 15	756	7.3	I	Stein, 1980a
<u>Osteodiscus cascadiae</u> 16	4	4.65	I	Stein, 1980a
<u>Paraliparis latifrons</u> 17	5	4.25	I	Stein, 1980a
<u>megalopus</u> 18	32	4.0	I	Stein, 1980a
<u>rosaceus</u> 19	1277	3.5	II	Stein, 1980a
<b>Macrouridae</b>				
<u>Coryphaenoides acrolepis</u> 20	70000	2.05	II	Stein & Percy, unpublished
<u>armatus</u> 21	2.5x10 <sup>6</sup>	ca.0.4	II	Stein & Percy, unpublished
<u>carapinus</u> 22	81400	0.64	II	Haedrich & Polloni, 1976
<u>filifer</u> 23	26000	1.9	II	Stein & Percy, unpublished
<b>Moridae</b>				
<u>Antimora rostrata</u> 24	1.1x10 <sup>6</sup>	0.75	II	Wenner, 1978
<b>Synphobranchidae</b>				
<u>Synphobranchus kaupi</u> 25	76400	1.2	II	Wenner, 1978
<b>Zoarcidae</b>				
<u>Lycenchelys atlanticus</u> 26	89	5.9	I	Wenner, 1978
<u>mirabilis</u> 27	44	4.2	I	Wenner, 1978
<u>paxillus</u> 28	30	3.0	I	Musick, Wenner & Sedberry, 1975
<u>Lycodes frigidus</u> 29	500	7.0	I	Johnsen, 1921
<u>Pachycara obesum</u> (33)	67	4.3	I	M.E. Anderson, pers. comm.
<u>Derepodichthys alepidotus</u> (34)	25	2.25	I	M.E. Anderson, pers. comm.
<u>Lycenchelys alba</u> (35)	38	3.1	I	M.E. Anderson, pers. comm.
<u>bellingshauseni</u> (36)	69	3.8	I	M.E. Anderson, pers. comm.
<u>jordani</u> (37)	38	5.2	I	M.E. Anderson, pers. comm.

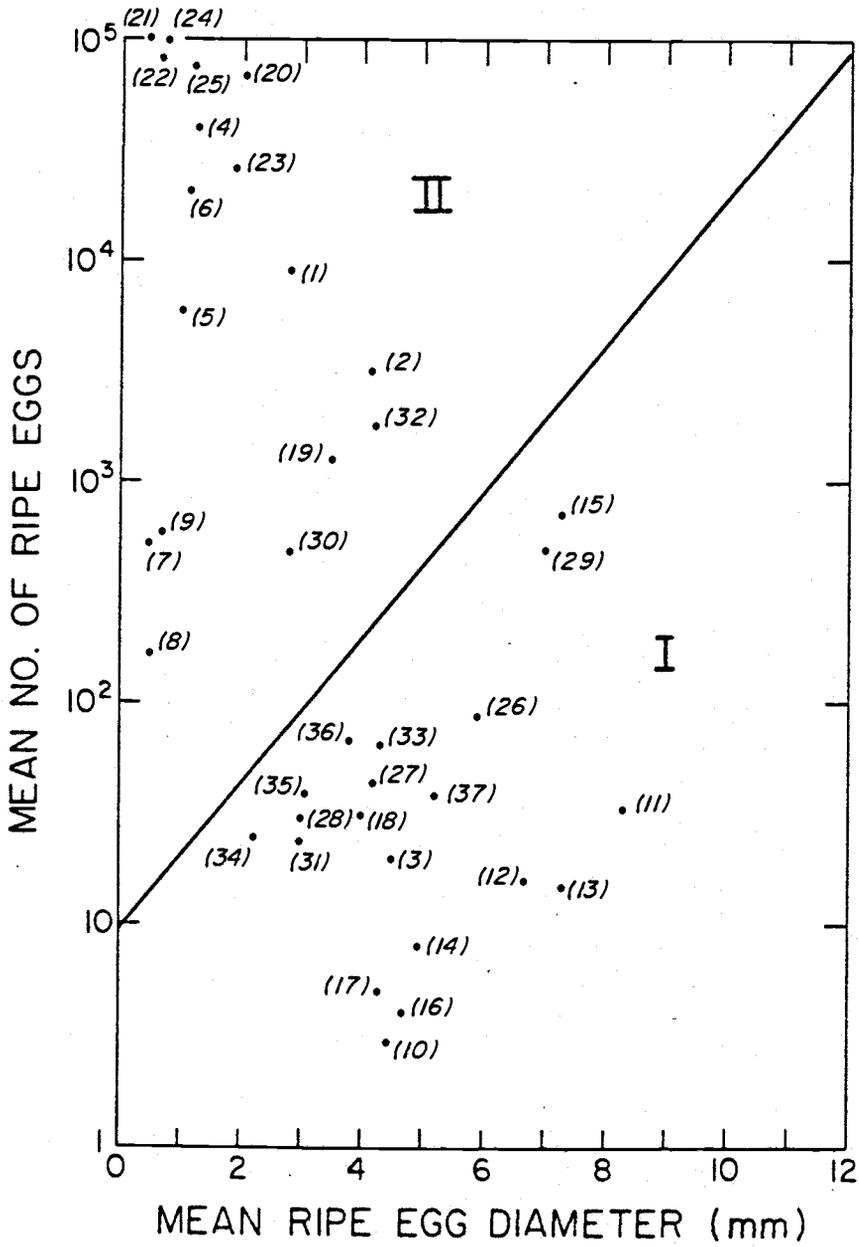


Figure 1. Mean ripe egg number vs. mean ripe egg diameter for fish species living below 2000 m. Numbers in parentheses refer to species listed in Table I.

rosaceus) "higher" fishes appear only in Group I. Inclusion of the aphyonids (a "middle" family) in Group I does not change the phylogenetic composition of the groups. Most of the members of Group I (usually secondarily deep-sea fishes) are from Division VII of Breder and Rosen (1966). Members of this division generally lack spawning migrations, and have benthic reproduction, parental care and demersal adhesive eggs or eggs with special characters. These deepwater benthic fishes have reproductive adaptations similar to those of shallow water species of the same families (except in the Alepocephalidae, which have no shallow water representatives). The members of Group II (usually ancient deep-sea fishes) are from Divisions I, II, and VI of Breder and Rosen (1966), which may have extensive spawning migrations, generally have pelagic eggs, and lack parental care. Most of these families have no shallow water representatives. There does not seem to be a single continuum represented by egg size and fecundity, but rather two distributions, representing groups of different phylogenetic composition.

I suggest that many of these secondarily deep-water fishes (most of Group I) were preadapted in shallow waters to deep-sea benthic life by possession of reproductive adaptations that help ensure maximal survival of the offspring. Rather than being simply another characteristic of secondarily deep-sea fishes, reproductive adaptations such as those occurring in liparidids (Stein, 1980a) enabled radiation of these species from shallow into deep water. These adaptations include low fecundity, very large eggs, direct development of the young, and parental care. Adaptations such as these may be rare in the pelagic for several reasons. First, large, yolky eggs tend to sink, although there are pelagic eggs larger than 4.0 mm (Ginzburg, 1968). Secondly, it is much more difficult to hide or camouflage pelagic eggs. Thirdly, there are few methods for parental care, although it is possible (Breder and Rosen, 1966; Balon, 1975). Finally, if parental care occurs the eggs must remain with the parent, so that offspring survival is directly linked with adult survival. This seems a risky proposition in the deep pelagic realm, where carnivory and predation are the predominant feeding modes of nekton.

Viviparity is apparently rare in deep-sea fishes. Only one family of deep-sea teleosts is known to have viviparous members: the benthic and benthopelagic Aphyonidae (Nielsen, 1969). In pelagic fishes viviparity is probably rare because internal fertilization, required by viviparity and ovoviviparity, necessitates development of copulatory organs, which in turn requires more energy (food). Ovoviviparity requires much larger eggs and viviparity requires direct parental nutrition of the embryos because the young are born into a food-poor environment and must be able to fend for themselves immediately. In benthic fishes viviparity is probably rare for other reasons. As pointed out above, viviparous adults must survive until birth of the offspring, whose development requires a continuous food supply. If food supplies are irregular, either the adult may not survive to bear the young (ovoviviparity, viviparity) or the embryos may not survive to term (viviparity). In oviparity, development need not be continuous (Braekevelt and McMillan, 1967), and once spawned and fertilized, the embryo is less dependent upon survival of the parent.

Competition in the pelagic zone and reproductive preadaptation of many shallow water benthic fish groups to deep sea life could have resulted in these differences in phylogenetic composition and reproductive mode. The protacanthopterygian fishes, which evolved earlier than the Paracanthopterygii and Acanthopterygii, probably became the dominant forms in the deep pelagic zone before the appearance and diversification there of the more advanced groups. Parin (1968) suggested that most of the deep-water pelagic fishes are derived from ancient Malacopterygii "subsequently displaced...by the more highly organized Acanthopterygii..". A few deep pelagic fishes (brotulids, macrourids, anglerfishes) were later derived from benthic forms. Below the relatively food-plentiful epipelagic zone is a region where food becomes increasingly sparse with greater depths. Most of the fishes of this region are small (the "Lilliputian" fauna of Murray and Hjort (1912)) and many are apparently inactive during the day (Barham, 1970). The energy conserving adaptations they developed are extreme and unlikely to be easily surpassed. Consequently, few later evolving groups would be able to coexist with

them or utilize different niches in the same zone. One of the most successful "advanced" groups to do so is the ceratioid anglerfishes, many of which have a highly effective and unique reproductive adaptation (sexual parasitism of the females by males). The efficacy of this adaptation, plus the associated feeding adaptations involving lures for prey, may be judged by the diversity of species within the group: 10 families, with about 100 species (Marshall, 1979).

As discussed above, the members of Group II are ancient deep-sea fishes (macrourids, eels, etc.). Presumably, these evolved prior to the "invasion" of the benthos by Group I families, and exploited the benthos early. They apparently do not differ in reproductive strategies from the pelagic fishes. They have high relative fecundities, lack parental care, and some are hermaphrodites. At least some species of macrourids (and bathysaurids?) have ontogenetic migrations from the epipelagic zone, where the eggs hatch, to the benthos (Johnson, 1974; Marshall, 1979; Merrett, 1978; Stein, 1980b). Most of the macrourids are benthopelagic (Marshall and Merrett, 1977) as are some notacanth and halosaurs (Marshall and Merrett, op. cit.). On the other hand, others, such as the brotulids, seem to be benthic. The Group I members presumably competed with the earlier arrivals for space or food. It is interesting to note that most or all of the "benthic" secondarily deep-sea fishes are true benthic species which rest on the bottom rather than live just above it, suggesting that the benthopelagic groups left little room or opportunity for new arrivals. Competition with the primary benthic and benthopelagic groups may well have limited the successful secondarily deep-sea fishes to those which a) were benthic rather than benthopelagic, and b) had reproductive adaptations which maximized offspring survival by increasing size and maturity of young at time of hatching (Marshall, 1953).

The abyssal benthic environment has long been considered to be one of the stablest known (Sanders and Hessler, 1969; Menzies, George, and Rowe, 1973; Marshall, 1979). It is a "K-selected" environment in the sense of Pianka (1970) and its organisms seem to be characterized by long life, slow development, late maturity, and iteroparity. Competition

is thought to be high (Sanders, 1968; Grassle and Sanders, 1973). The near-surface pelagic zone is usually considered to be a much more "r-selected" environment, where physical factors, such as temperature, light, and nutrients, and biological factors, such as plankton biomass, vary during the year. Species living near the surface often are characterized by short lives, early maturity, rapid development, and semelparity. Competition is variable. The fishes living in the deep-sea benthos display two different reproductive strategies, and in doing so utilize both environments. The fishes in Group I (liparidids, for example) have maximized offspring survival by increasing egg size to produce demersal eggs from which (probably) very well developed young hatch. These young are better able to survive (Marshall, 1953) and are not subjected to any environment other than the one in which the adults live. Fishes in Group II (macrourids and eels, for instance) have a high relative fecundity and relatively small pelagic eggs which probably develop near the surface. Larval mortality is high, and the young must make a dangerous ontogenetic migration before recruitment to the benthic population. Thus, the adult abyssal benthic fishes live in a K-selected environment, but while individuals of the species in Group I spend their entire lives there, individuals of many of the species of Group II spend their early lives in a quite different, more r-selected environment. This difference may serve to reduce competition among the larvae for scarce food in the deep-sea benthos, and the ontogenetic migrations of members of Group II may serve as a mechanism by which energy from the relatively food rich photic zone is transferred to the abyssal depths. Conversely, the pelagic eggs of members of the same group may act as a mechanism transferring energy from the deep sea back to near surface waters.

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