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### THE DEVELOPMENT AND OCCURRENCE OF LARVAE OF THE LONGFIN IRISH LORD, *HEMILEPIDOTUS ZAPUS* (COTTIDAE).

The subfamily Hemilepidotinae, endemic to the North Pacific Ocean, is one of the more generalized subfamilies within the Cottidae (Peden 1978). According to Peden (1978), the subfamily is composed of three subgenera: 1) *Calycilepidotus* which includes *Hemilepidotus spinosus*; 2) *Hemilepidotus* which includes *H. hemilepidotus*, *H. jordani*, *H. zapus*, and *H. gilberti*; and 3) *Melletes* which includes *H. papilio*. The early life histories of most species are inadequately known and separation of larvae in mixed samples is difficult. Gorbunova (1964) described a number of larval series which she labeled *H. hemilepidotus*, *H. gilberti*, *H. gilberti zapus*, *H. jordani*, and *H. papilio*,<sup>1</sup> but these descriptions are incomplete as well as incorrect for several species (Peden 1978; Richardson and Washington 1980). Hattori (1964) described a series of *H. gilberti* larvae (7.1-32.5 mm), and Peden (1978) illustrated postlarvae (> 18 mm) of *H. hemilepidotus*, *H. spinosus*, *H. zapus*, and *H. jordani*. Richardson and Washington (1980) described larvae of *H. hemilepidotus* and *H. spinosus*. We here provide the first complete description of *H. zapus* larvae, and include comments on larval occurrence in the eastern Bering Sea. This work supplements and clarifies the work of previous researchers by providing diagnostic characters useful in distinguishing the species.

#### MATERIALS AND METHODS

Specimens of *H. zapus* used in this study were collected during ichthyoplankton surveys conducted in the Bering Sea by the Northwest and Alaska Fisheries Center between 1977 and 1980. Morphological

measurements were made on 57 unstained larvae (6.7-22.0 mm SL) following Matarese et al. (1981), except depth at caudal peduncle which was measured at the point of least depth. Measurements were grouped by 1 mm SL intervals, and the means of the measurements within each interval were plotted as percentage of the mean of standard lengths or head lengths within the interval (Kendall and Vinter 1984). A computer-generated best nonparametric curve, based on all data points, was drawn to illustrate relative growth trends. Counts of meristic structures were made on 13 specimens differentially stained according to Dingerkus and Uhler (1977) following procedures outlined in Matarese et al. (1981). Terminology of head spination generally follows Richardson and Laroche (1979) and Richardson and Washington (1980). Illustrations were made by the junior author with a camera lucida, and all specimens were preserved in either 3% Formalin<sup>2</sup> buffered with sodium borate or 100% glycerin.

#### Identification of *Hemilepidotus zapus*

We have routinely collected three types of Hemilepidotinae larvae during ichthyoplankton surveys in the eastern Bering Sea (1977-80). According to Peden (1978), four species of adults occur in this area: *Hemilepidotus hemilepidotus*, *H. jordani*, *H. zapus*, and *H. papilio*. Although preflexion larvae of *H. hemilepidotus* and *H. jordani* cannot presently be separated, we can separate the two species at notochord flexion according to differences in external pigment along the posterior body. *Hemilepidotus hemilepidotus* larvae develop pigment above the notochord along the posterior body earlier and in greater density than larvae of *H. jordani* (Fig. 1A, B). Initially, the third series of larvae (< 17.0 mm SL) was misidentified as *H. papilio* (see Waldron and Vinter<sup>3</sup>) based on the presence of urostyle pigment (Gorbunova 1964). With the acquisition of larger specimens, > 17.0 mm SL, the complete series was later identified as *H. zapus* based on a set of characters taken in part from Peden (1978) (Table 1). Gorbunova's (1964) specimen attributed to *H. zapus* lacks pigment on the urostyle; of her two illustrations of *H. papilio* (footnote 1) only the 10.7 mm SL

<sup>2</sup>References to trade names do not imply endorsement by the National Marine Fisheries Service, NOAA.

<sup>3</sup>Waldron, K. D., and B. M. Vinter. 1978. Ichthyoplankton of the eastern Bering Sea. Unpubl. manuscr., 77 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Boulevard E., Seattle, WA 98112.

<sup>1</sup>*Hemilepidotus papilio* (= *Melletes papilio* from Gorbunova (1964)).

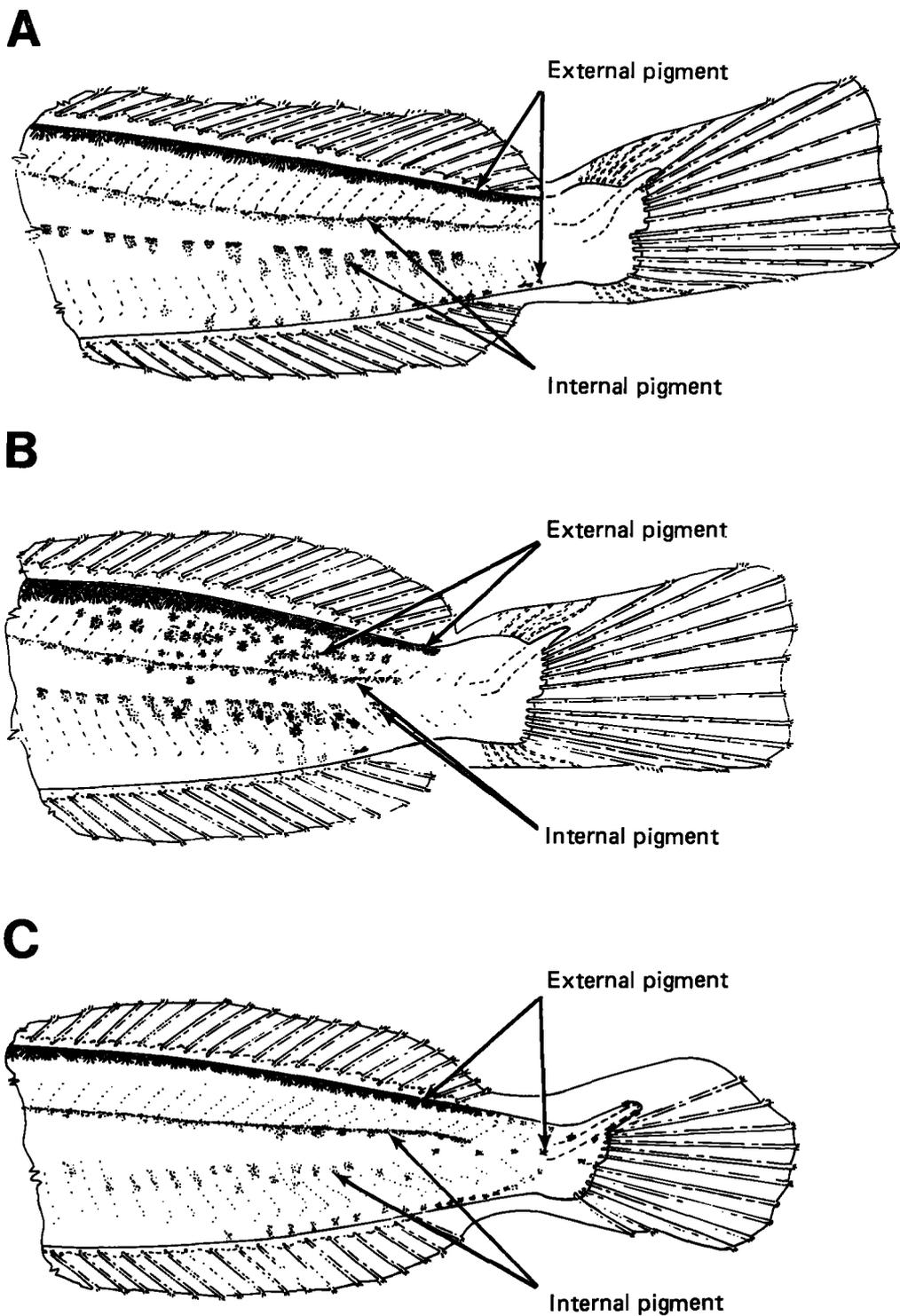


FIGURE 1. – Postanal pigment patterns in *Hemilepidotus* larvae: A) *H. jordani*, 13.7 mm SL; B) *H. hemilepidotus*, 12.7 mm SL; C) *H. zapus*, 12.6 mm SL.

TABLE 1.—Comparison of some important differentiating characters in *Hemilepidotus zapus* and *H. papilio*.

Characters	This study	<i>H. zapus</i> <sup>1</sup>	<i>H. papilio</i> <sup>1</sup>
Dorsal spines	X-X1	X1 (X1-X11)	X11 (X1-X111)
Pectoral fin rays	16-17	16 (15-17)	17-18 (16-18)
Total soft fin rays; dorsal, anal, and both pectoral fins	71	67-76	69-74
Lateral line pores	54-56	52 (47-58)	59 (49-65)
Number of vertebrae	37-38	37-38	40
Number of horizontal scale rows in ventral band	ca. 8	8 or 9	ca. 4
Dorsal fin notch between third and fourth spine	yes	yes	no

<sup>1</sup>Data are from Peden (1978); mean is followed by range in parentheses.

larvae is *H. zapus*, while the 13.7 mm SL larva lacks urostyle pigment and is probably *H. jordani*.

Early larvae of *H. zapus* (6.5-17.0 mm SL) were linked together by the presence of melanophores above and below the urostyle (Figs. 1C, 2); such melanophores are lacking in all other known Hemilepidotinae larvae. Larvae undergoing notochord flexion can be distinguished from *H. hemilepidotus* by the lack of external pigment along the posterior body and from *H. jordani* by the presence of ventral midline pigment which curves up toward the urostyle (Fig. 1).

After notochord flexion and through the juvenile period, counts of meristic structures as well as a combination of adult characters (Peden 1978) will allow separation of the three species. Postflexion larvae of *H. zapus* have scales on the caudal peduncle that will distinguish them from other, similar-sized Hemilepidotinae larvae. These larvae also have a characteristic notch in the first dorsal fin, between the third and fourth spine, that is present in adults of all *Hemilepidotus* except *H. papilio* (Fig. 2F). A summary of some diagnostic features of all known *Hemilepidotus* larvae is presented in Table 2. Larvae and juveniles of *H. papilio* remain unknown.

### General Trends of Development

#### Pigmentation (Fig. 2)

In the smallest larvae (6-7 mm SL), pigment appears on the head dorsally over the midbrain and on the anterior forebrain. In larger larvae 7-9 mm SL, additional pigment appears at the base of the hindbrain, posterior to the eye and in the opercular area. In postflexion larvae, head pigment increases.

Separate pigment patches appear posterior to the eye (usually about 5 or 6 spots) and on the operculum dorsoposterior to the preopercular bone. Larvae 6-7 mm SL have pigment on the nape and on the dorsal surface of the gut. Gut pigment increases laterally with development, and in larger postflexion larvae it becomes more internal than external. By 14-15 mm SL, nape pigment extends ventrally to the dorsal surface of the gut.

There are five general areas of pigmentation in the postanal region: 1) an external row (appearing more or less double) of melanophores along the dorsal midline extending from the nape to the last myomere; 2) a dorsolateral row of internal pigment along the notochord, extending from the nape to about the last 4-7 myomeres; 3) an external row of melanophores along the ventral body midline from midbody (about 11 myomeres after anus) to the last myomere; 4) a ventrolateral row of internal pigment along the notochord, beginning at about 4-6 myomeres after the anus and extending to about 6 or 7 myomeres from the end of the tail; and 5) a few external melanophores along the notochord in the caudal peduncle area, and external melanophores dorsal and ventral to the notochord at the posterior tail tip. Prior to notochord flexion, at about 9.0 mm SL, the anterior ventral midline pigment gradually becomes more internal. In postflexion larvae, this ventral midline row is comprised of < 10 melanophores beginning about 17 myomeres posterior to the anus. By 16.7 mm SL, all the postanal pigment is internal except for the dorsal midline melanophores and a few spots in the caudal peduncle area. After about 17 mm SL, melanophores in the caudal peduncle are no longer visible.

#### Morphology (Table 3; Fig. 3)

Relative growth trends are summarized in Figure 3. Preanal length, head length, depth at pectoral fin, snout to anal fin length, and snout length increase with development. Eye diameter as a proportion of head length undergoes a gradual decrease with development. Depth at the caudal peduncle and the length from the snout to dorsal fin origin increase sharply with development in larvae about 16.0-19.0 mm SL and then decrease in larger specimens.

#### Meristic Structures (Tables 4, 5)

Branchiostegal rays have begun to ossify in our smallest specimens (7-8 mm SL), and the adult complement of six rays is completely ossified in larvae  $\geq$  12-13 mm SL.

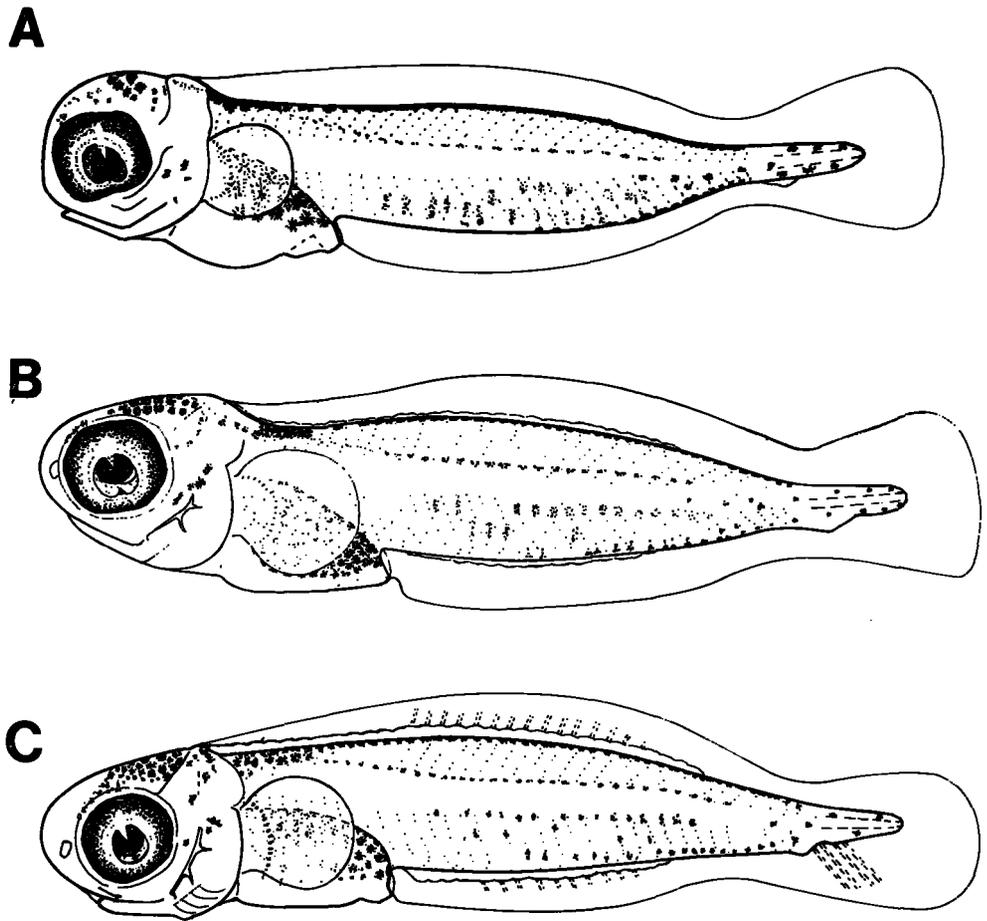


FIGURE 2. – Larvae of *Hemilepidotus zapus*: A) 6.7 mm SL; B) 8.7 mm SL; C) 11.0 mm SL;

**Fins**—All fin rays show their initial ossification in larvae between 12 and 13 mm SL. Fin formation occurs in the sequence: dorsal spines and fin rays, anal fin rays, and principal caudal fin rays (12-13 mm SL); pectoral fin rays (13-14 mm SL); pelvic spine and fin rays (15-16 mm SL); and secondary caudal fin rays (16-17 mm SL). The pterygiophores supporting dorsal fin rays begin ossifying at 16-17 mm SL, and those supporting anal fin rays begin ossifying at 17-18 mm SL. The largest specimen (20.0 mm SL) has completely ossified dorsal and anal pterygiophores.

**Axial skeleton**—Neural and haemal spines have started ossification in the smallest larvae 7-8 mm SL, and are fully ossified in larvae 15-16 mm SL. Abdominal vertebral centra are completely ossified in larvae

12-13 mm SL, but the caudal vertebral centra are not fully ossified until larvae are slightly larger at about 14-15 mm SL.

Lateral line scales do not begin ossifying until larvae are 18.0 mm SL, and our largest specimen (20.0 mm SL) has a fully ossified complement of scales.

**Spination** (Table 5)—The development of head spines is summarized in Table 5. The parietal and nuchal spines fuse in larvae > 13 mm SL and appear as a single spine in the larger larvae 18-20 mm SL. A postocular spine is ossified in larvae 12-13 mm SL but disappears by 18-20 mm SL. A small spine below the eye (infraorbital) ossifies by 14-15 mm SL, but is no longer visible in specimens 20 mm SL.

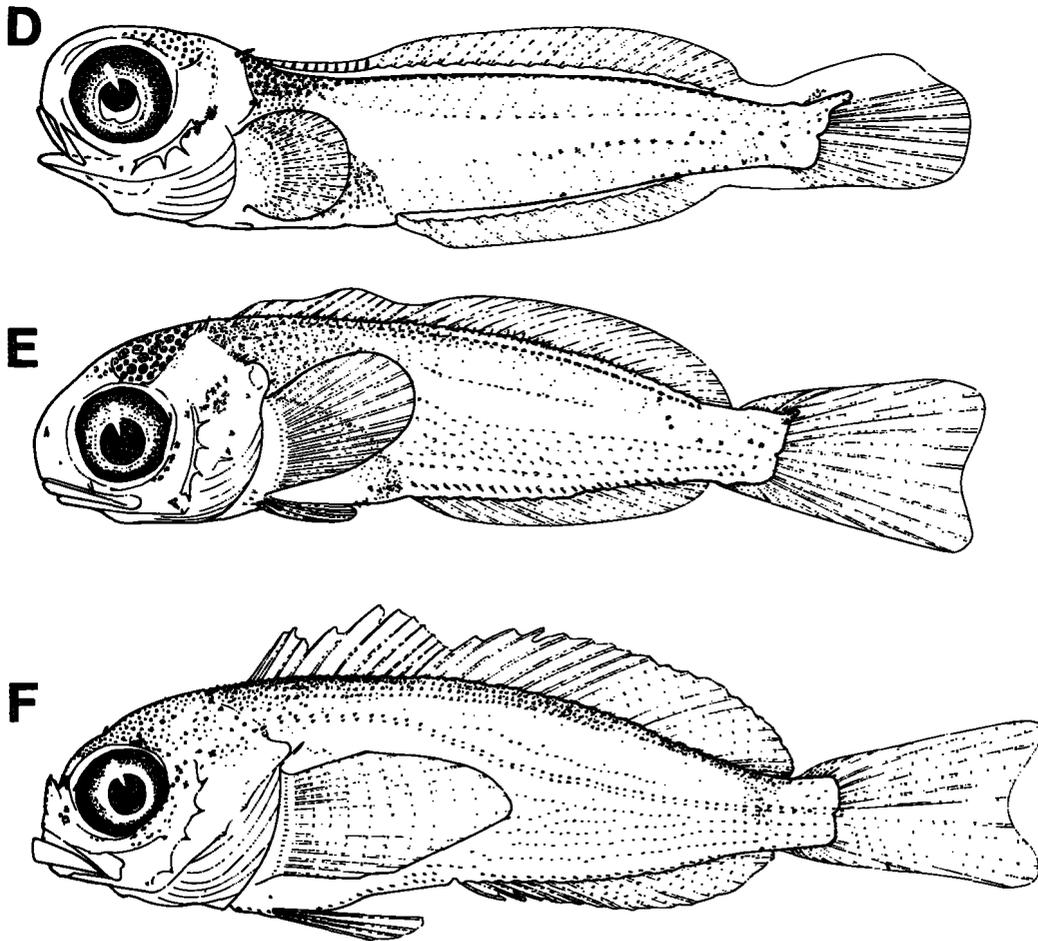


FIGURE 2.—Continued—D) 13.0 mm SL; E) 16.7 mm SL; F) 22.8 mm SL.

#### Occurrence of *Hemilepidotus zapus* in the Eastern Bering Sea

During 8 yr of sampling ichthyoplankton at a total of 250 stations in the eastern Bering Sea (in the approximate area between lat. 60°N and long. 174°W with more intensive sampling between the Pribilof Islands and Unimak Island), only 58 *Hemilepidotus zapus* larvae were collected. The number of positive stations is indicated in Figure 4.

Small *H. zapus* larvae (6.7-10.1 mm SL) were collected during winter in surface water north of the Pribilof Islands (Fig. 4A). Only a single larva (11.0 mm SL) was taken in February 1978 at the surface in about the same area over the slope (Fig. 4A). Our largest collection of larvae (12.2-16.7 mm SL) was

made in late April and early May (Fig. 4B). Most of the larvae were collected in neuston nets at stations over the slope, but in May a few larvae were taken over the continental shelf. Larvae primarily occurred south of the Pribilof Islands. The largest larvae (18-22 mm SL) were collected during June and July at scattered stations throughout the area including only one northwest of the Pribilof Islands (Fig. 4C).

Although data are insufficient to document the exact time and geographical extent of spawning, the presence of small larvae indicates some spawning occurs in early winter north of the Pribilof Islands. Peden (1978) indicated that adult and postlarval *H. zapus* have been collected only along the Aleutian Islands. Further studies are needed to investigate whether larvae and juveniles move south to the Aleu-

TABLE 2.—Selected postanal pigmentation characters useful in distinguishing preflexion and flexion *Hemilepidotus* larvae.

Taxon	Pigmentation characters							Diagnostic	Source
	Dorsal midline	Dorso-lateral	Above notochord (internal)	Below notochord (internal)	Ventro-lateral	Ventral midline	Caudal region		
<i>H. spinosus</i>	By 5 mm, a continuous line from head to posteriormost myomere, becoming heavier	By 6 mm, becoming heavier	By 8-9 mm, along length of body	Not obvious	By 6 mm, becoming heavier	From anus to posteriormost myomere, >15 melanophores	Sparse, ventral midline continuous	Lateral, ventral midline	Richardson and Washington 1980
<i>H. hemilepidotus</i>	Until 7 mm unpigmented area between myomeres 4-11, becoming moderately heavy	By 11 mm, moderate	By 6-7 mm, along length of body	By 8-9 mm, begins posterior to anus	By 11 mm, moderate	Begins 9-10 myomeres after anus, <15 melanophores	None	Lateral, lack of caudal pigment	Richardson and Washington 1980, This study
<i>H. jordani</i> <sup>1</sup>	Similar to <i>H. hemilepidotus</i> but not as heavy	None	Similar to <i>H. hemilepidotus</i>	Similar to <i>H. hemilepidotus</i>	Some internal only	By flexion, a few internal melanophores	None	Lack of lateral and caudal pigment	This study
<i>H. zapus</i>	Similar to <i>H. hemilepidotus</i> but not as heavy	None	By 6 mm, along length of body	By 8 mm, incomplete, begins posterior to anus	Some internal only	Begins 11 myomeres after anus, <15 melanophores	Ventral midline continues, above and below urostyle	Urostyle	This study
<i>H. gilberti</i>	Pigment begins 8-9 myomeres after anus	None	None <sup>2</sup>	None <sup>2</sup>	None	Begins 10 myomeres after anus, <15 melanophores	None	Unpigmented area along dorsal midline, lack of lateral pigment	Hattori 1964

<sup>1</sup>Preflexion larvae of *H. hemilepidotus* and *H. jordani* cannot presently be separated.

<sup>2</sup>No internal pigment is shown on Hattori's figures.

TABLE 3.—Morphometrics (in millimeters) of larvae and juveniles of *Hemilepidotus zapus*. Specimens between dashed lines are undergoing notochord flexion.

Standard length	Total length	Preanal length	Head length	Snout length	Eye diameter	Depth at pectoral fin	Depth at caudal peduncle	Snout to dorsal	Snout to anal fin
6.5	6.9	2.4	1.3	0.1	0.8	1.3			
6.7	7.4	2.4	1.3	0.1	0.8	1.3			
6.7	7.2	2.4	1.3	0.1	0.8	1.3			
7.1	7.5	2.7	1.4	0.1	0.8	1.3			
7.1	7.7	2.8	1.3	0.1	0.9	1.3			
7.3	7.8	2.7	1.4	0.1	0.9	1.4			
7.6	8.2	2.7	1.3	0.1	0.9	1.4			
7.7	8.3	2.7	1.3	0.1	0.9	1.5			
8.2	8.9	3.1	1.7	0.2	1.0	1.5			
8.2	8.9	3.2	1.8	0.2	1.0	1.6			
8.5	9.1	3.3	1.9	0.3	1.0	1.6			
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8.7	9.5	3.5	2.0	0.3	1.1	1.7			
8.7	9.4	3.4	2.0	0.3	1.1	1.7			
9.1	9.8	3.6	1.9	0.3	1.0	1.7			
9.2	10.0	3.6	2.1	0.2	1.1	1.7			
9.2	9.8	3.6	1.9	0.2	1.1	1.7			
9.3	10.1	3.9	2.1	0.2	1.1	1.7			
9.5	10.1	4.0	2.1	0.3	1.2	1.8			
9.8	10.5	3.6	1.9	0.2	1.1	1.7			
10.1	10.9	4.0	2.3	0.3	1.2	1.8			
11.0	12.0	4.4	2.6	0.3	1.3	2.1			
12.0	13.5	5.5	3.2	0.6	1.4	2.5	1.0	3.0	5.8
12.2	14.3	5.5	3.3	0.5	1.5	2.5	0.9		5.8
12.2	14.0	5.6	3.4	0.5	1.5	2.6	0.9	3.3	5.9
12.3	14.4	5.6	3.3	0.4	1.5	2.6	1.0	3.2	5.9
12.6	14.5	5.8	3.3	0.5	1.5	2.8	1.1	3.3	6.0
12.9	15.0	5.7	3.5	0.6	1.5	2.7	1.1	3.3	6.1
12.9	14.6	5.6	3.4	0.4	1.5	2.6	1.0	3.4	6.0
13.0	15.0	5.6	3.7	0.6	1.5	2.6	1.1	3.3	6.0
13.0	15.2	5.6	3.5	0.6	1.6	2.7	1.1	3.3	6.0
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13.2	15.4	5.5	3.5	0.6	1.6	2.9	1.1	3.4	5.9
13.5	16.0	6.0	3.5	0.6	1.6	2.8	1.2	3.5	6.4
13.6	16.0	5.9	3.7	0.6	1.5	2.8	1.2	3.3	6.3
13.8	16.1	5.9	3.7	0.6	1.7	3.0	1.2	3.4	6.3
14.0	16.7	6.3	3.7	0.6	1.8	3.2	1.3	3.7	6.6
14.3	17.1	6.5	3.9	0.6	1.8	3.1	1.3	3.7	6.9
14.4	17.2	6.8	4.0	0.6	1.9	3.2	1.4	4.0	7.1
14.5	17.2	6.9	4.0	0.7	1.9	3.3	1.4	4.1	7.2
14.7	17.5	6.8	3.9	0.6	1.9	3.2	1.3	3.8	7.1
14.9	17.9	7.0	4.0	0.6	1.8	3.3	1.4	4.0	7.2
14.9	18.0	7.0	4.1	0.6	2.0	3.4	1.5	4.2	7.3
15.1	18.6	7.2	4.3	0.7	2.0	3.7	1.6	4.2	7.5
15.2	18.3	7.2	4.5	0.7	2.1	3.7	1.6	4.2	7.5
15.3	19.0	7.5	4.7	0.8	2.0	3.9	1.6	4.4	7.8
15.5	19.0	7.3	4.5	0.8	2.0	3.8	1.6	4.5	7.6
15.6	19.0	7.4	4.6	0.7	2.0	3.8	1.6	4.3	7.7
15.9	19.7	7.8	4.7	0.8	2.1	3.9	1.7	4.6	8.1
16.7	20.7	7.9	5.1	0.8	2.1	4.3	1.8	4.8	8.2
16.8	21.3	8.1	5.4	0.8	2.3	4.5	1.7	5.1	8.5
16.9	20.9	8.2	5.2	0.8	2.2	4.4	1.7	5.0	8.6
18.0	23.0	9.0	6.2	1.0	2.3	5.5	1.9	5.2	9.3
19.1	25.0	9.8	6.3	1.0	2.3	5.6	2.0	5.4	10.0
19.3	24.9	10.1	7.0	1.3	2.6	5.7	1.9	6.1	10.5
20.5	26.0	10.5	6.7	1.3	2.5	6.2	2.0	5.5	10.9
21.0	26.5	10.9	7.0	1.3	2.5	6.3	2.1	5.7	11.1
21.0	26.6	11.1	7.0	1.5	2.5	6.3	2.0	6.0	11.5
21.2	27.0	11.4	7.2	1.6	2.5	6.5	2.0	6.1	11.6
22.0	27.5	11.5	7.3	1.3	2.6	6.7	2.1	6.0	11.9

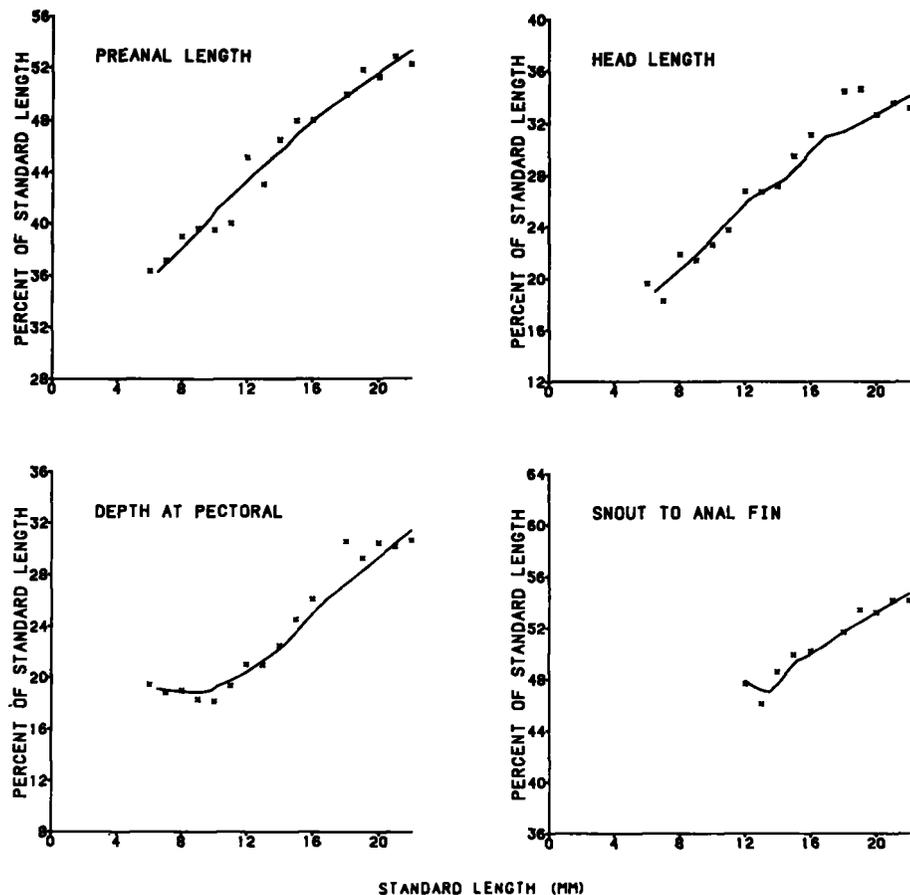


FIGURE 3.—Relative trends in selected morphometric features

TABLE 4.—Development of meristic characters in larvae of *Hemilepidotus*

Size interval (mm SL)	Sample size	Fin rays						
		Dorsal	Anal	Pectoral	Pelvic	Caudal		Total
						Principal	Secondary	
7-8	2							
8-9	3							
9-10	2							
10-12	—							
12-13	3	X,11-21	17	8-10	1,0	12	3-5	15-17
13-14	1	XI,21	17	16	1,3	12	9	21
14-15	3	X-XI,20-21	17	13-16	1,3	12	9	21
15-16	2	X,21	17	16	1,4	12	11-13	23-25
16-17	1	XI,20	17	17	1,4	12	15	27
18	1	XI,20	16	16	1,4	12	15	27
20	1	XI,21	17	16	1,4	12	14	26

<sup>1</sup>Specimens in this size group did not accept alizarin stain.

<sup>2</sup>Haemal spines 23-24 are fused.

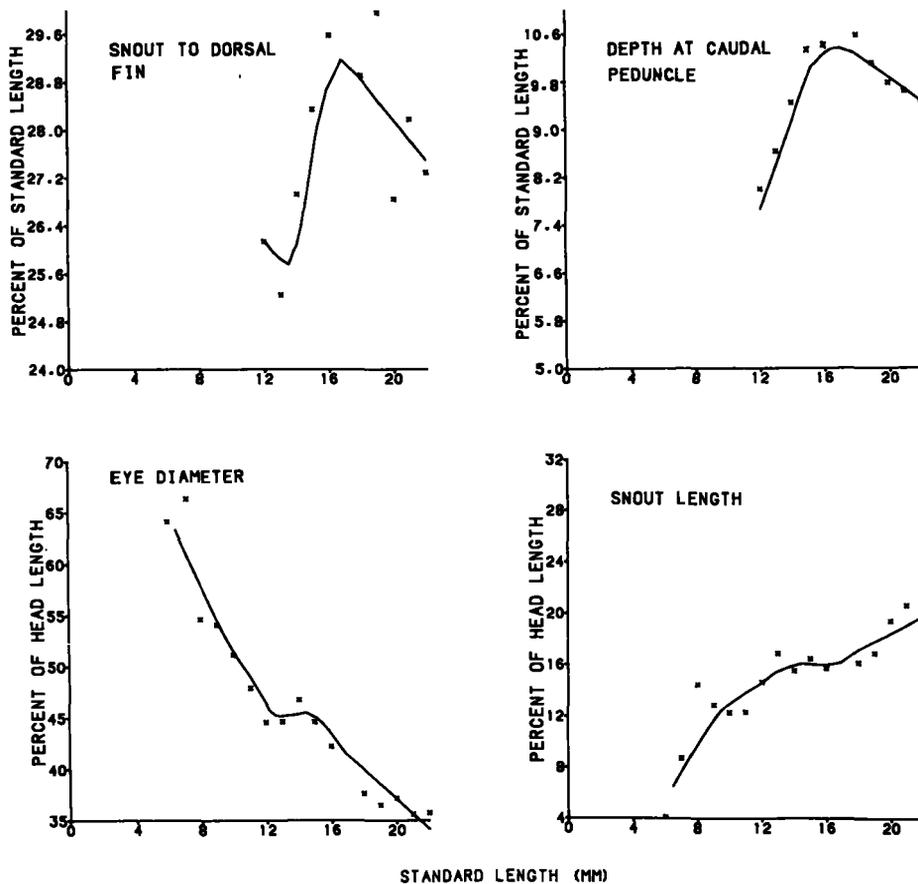


FIGURE 3.—Continued—during ontogeny in *Hemilepidotus zapus*.

*zapus*. Specimens below the dashed line have completed notochord flexion.

Size interval (mm SL)	Sample size	Pterygophores		Axial skeleton				Branchiostegal rays	Lateral line scales
				Spines		Centra			
		Dorsal	Anal	Neural	Haemal	Precaudal	Caudal		
7-8	2			12-19	9			2-3	
8-9	3			20	10			4	
9-10	2			29	17			5	
10-12	—								
12-13	3			35	22	12	23	6	
13-14	1			36	23	12	25	6	
14-15	3			36	24	12	24-26	6	
15-16	2			37	25	12	26	6	
16-17	1	15		37	24	12	25	6	
18	1	30	16	37	25	12	26	6	54
20	1	31	17	37	24	12	26	6	56

TABLE 5.—Development of spines in the head region of *Hemilepidotus zapus* larvae. Specimens below the dashed line have completed notochord flexion.

Size interval (mm SL)	Sample size	Parietal	Nuchal	Preopercular	Opercular	Postopercular	Superior infra-orbital	Nasal	Articular	Cleithral	Post-temporal supra-cleithral
7-8	2	0-1		2							
8-9	3	1		3							
9-10	2	1		3							
10-12											
12-13	3	<sup>2</sup> 1	<sup>2</sup> 1	4		1			1		1-2
13-14	1	<sup>2</sup> 1	<sup>2</sup> 1	4		1		1	1		2
14-15	3	<sup>2</sup> 1	<sup>2</sup> 1	4	3	1	1	1	1		2
15-16	2	<sup>2</sup> 1	<sup>2</sup> 1	4	3	1	1	1	1		<sup>3</sup> 3
16-17	1	<sup>2</sup> 1	<sup>2</sup> 1	4	3	1	1	1	1	1	<sup>3</sup> 3
18	1		1	4	3	0	1	1	1	1	<sup>3</sup> 3
20	1		1	4	3	0	0	1	<sup>2</sup> 1	1	<sup>3</sup> 3

<sup>1</sup>Specimens in this size group did not accept alizarin stain.

<sup>2</sup>Spines are beginning to fuse at base but points can still be observed.

<sup>3</sup>Spine(s) reduced in size.

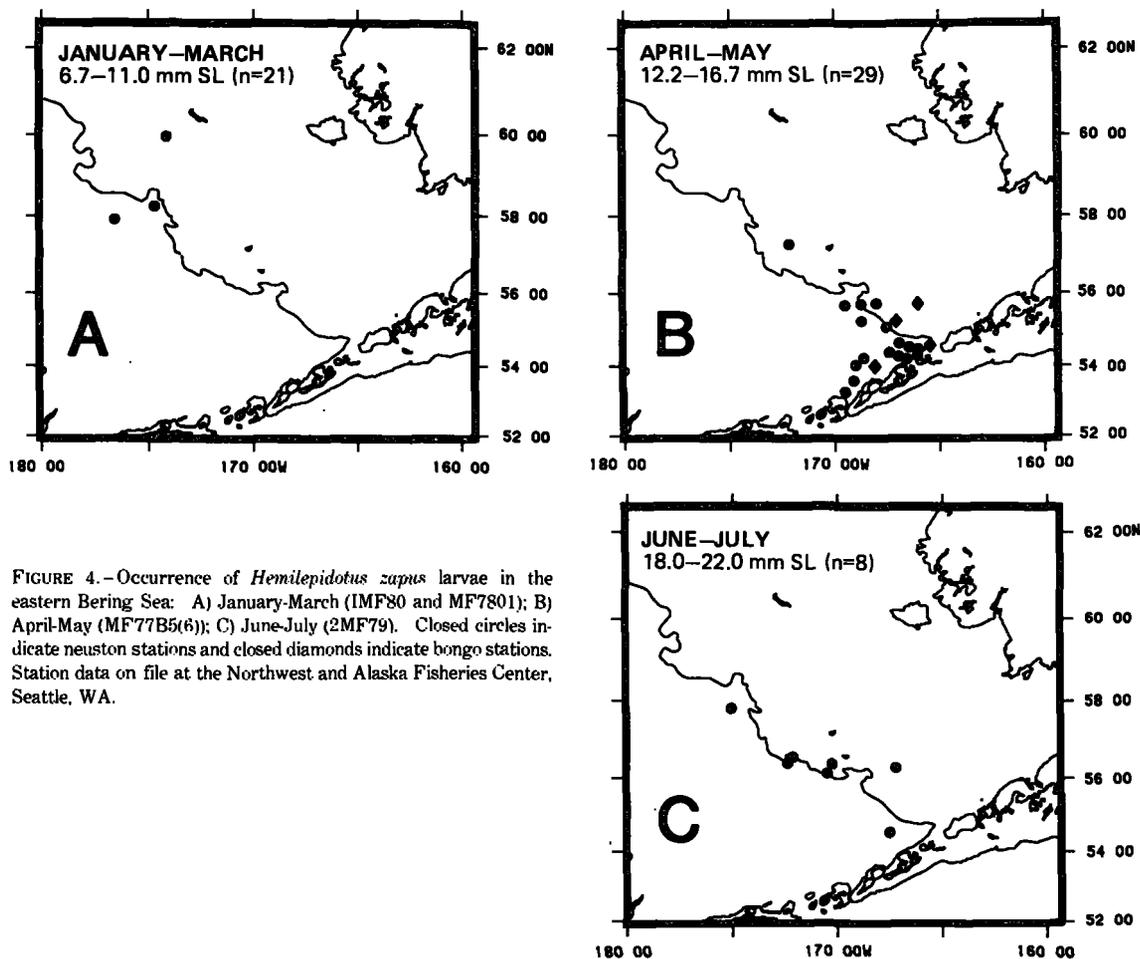


FIGURE 4.—Occurrence of *Hemilepidotus zapus* larvae in the eastern Bering Sea: A) January-March (IMF80 and MF7801); B) April-May (MF77B5(6)); C) June-July (2MF79). Closed circles indicate neuston stations and closed diamonds indicate bongo stations. Station data on file at the Northwest and Alaska Fisheries Center, Seattle, WA.

tians or whether adult *H. zapus* range further north.

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#### AN APPROACH TO ESTIMATING AN ECOSYSTEM BOX MODEL

Recent trends in ecosystem modeling have produced complex simulation models which are very data intensive (Andersen and Ursin 1977; Laevastu and Larkins 1981). However, in many situations the construction of a biomass budget for a box model of an ecosystem is relatively simple and can provide important information about the ecosystem standing stock and energy flow (Walsh 1981; Pauly 1982; Polovina 1984).

The ECOPATH model is an analytical procedure to estimate a biomass budget for a box model of an ecosystem given inputs which specify the components of the ecosystem, together with their mortality, diet, and energetics value. A computer program for ECOPATH has been written in BASIC-80, version 5.21, by Microsoft<sup>1</sup> (CP/M version). A listing of the ECOPATH computer program and a user's manual are available from the author.

The ECOPATH model produces estimates of mean annual biomass, annual biomass production, and annual biomass consumption for each of the user specified species-groups. The species-groups represent aggregations of species with similar diet and life history characteristics and which have a common physical habitat. The ECOPATH model is not a simulation model with a time component as are some more complex ecosystem models. It estimates a biomass budget for the marine ecosystem in a static situation under the assumption that the ecosystem is at equilibrium conditions.

Equilibrium conditions are defined to exist when the mean annual biomass for each species-group does not change from year to year. This condition results in a system of biomass budget equations which, for species-group *i*, can be expressed as

$$\text{Production of biomass for species } i - \text{all predation on species } i - \text{nonpredatory biomass mortality for species } i - \text{fishery catch for species } i = 0 \text{ for all } i. \quad (1)$$

The ECOPATH model expresses each term in the budget equation as a linear function of the unknown mean annual biomasses ( $B_i$ 's) so the resulting biomass budget equations become a system of simultaneous equations linear in the  $B_i$ 's. The mean annual biomass estimates are obtained by solving the system of simultaneous linear equations.

<sup>1</sup>Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.