

Abstract.—Pelagic larval summer flounder, *Paralichthys dentatus*, were collected in the NW Atlantic Ocean from 1985 to 1993, and their feeding habits were examined in relation to larval stage. Collections included preflexion, flexion, premetamorphic, and metamorphic larvae, although preflexion larvae composed the bulk of the specimens. Incidence of feeding and gut-fullness data indicated that larvae began feeding near sunrise and continued feeding throughout daylight hours. Incidence of feeding reached its lowest point, 8.3%, at 0400–0559 hours, then dramatically increased to 54.6% at 0600–0759. Maximum gut fullness was seen between 1200 and 1559. The only time during which all larvae contained prey in their guts was 0800–0959. Immature copepodites were the primary prey for all oceanic larval stages. In addition, small prey, such as tintinnids and copepod nauplii, made major contributions to the preflexion diet, and large prey, such as calanoid copepods and appendicularians, made major contributions to the diets of premetamorphic and metamorphic larvae. Metamorphic larvae were also collected as they entered a New Jersey estuary, at night, and their diet was examined. At 1800–1959 and 2000–2159 hours, the incidence of feeding in estuarine larvae was significantly lower than in oceanic larvae. The estuarine diet was dominated by the calanoid copepod, *Temora longicornis*. Incidence of feeding was observed to decline as metamorphosis progressed, from 19.1% at stage G to 2.9% at stage H. However, this apparent cessation in feeding, when the right eye was at the midpoint of migration, may not bring about undue ecological peril to summer flounder larvae.

Feeding habits of pelagic summer flounder, *Paralichthys dentatus*, larvae in oceanic and estuarine habitats

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The summer flounder, *Paralichthys dentatus*, an important component of recreational and commercial fisheries over the continental shelf and in estuaries of the Middle Atlantic Bight (United States), is currently overexploited. Evidence of this includes a drastic reduction in both commercial and recreational landings, in relation to peak years, and compressed age structure (Able and Kaiser, 1994). Both the fishery's decline and efforts to culture summer flounder (Bengtson et al., 1994; Bengtson and Nardi, 1995) are reviving interest in the basic biology of this species. Although much is known about the early life history of summer flounder, beginning with a description of eggs and larvae (Smith and Fahay, 1970) and including the timing of spawning, offshore distribution of eggs and larvae (Smith, 1973; Able et al., 1990), inshore occurrence of larvae and juveniles (Able et al., 1990), patterns of metamorphosis (Keefe and Able, 1993), and settlement processes (Burke et al., 1991; Keefe and Able, 1994; Norcross and Wyanski, 1994), many gaps still exist in our collective knowledge of larval and early-juvenile ecology.

Because survival beyond the early life history stages is based on an "eat and not be eaten" strategy (Keenleyside, 1979; Olla and Davis, 1988; Olla et al., 1994), feeding hab-

its clearly define much of larval and early-juvenile ecology. Recently, larval summer flounder studies have focused on the effects of delayed feeding on survival and growth (Bisbal and Bengtson, 1995a), describing the starving condition (Bisbal and Bengtson, 1995b) and the development of the digestive tract (Bisbal and Bengtson, 1995c). Although these studies examined natural rates and processes, they were all conducted on larvae that were reared in a laboratory. Most of what is known about the early feeding ecology of wild summer flounder has been derived from metamorphosing larvae and early juveniles that were captured with benthic trawls in estuarine nursery habitats (Burke, 1995). Beyond the patent inference that planktonic larvae ingest plankton (e.g. Morse, 1981), very little is known regarding the early pelagic feeding ecology of this species (Rogers and Van Den Avyle, 1983; Grimes et al., 1989).

This study considers feeding ecology of larval summer flounder collected in pelagic habitats in the NW Atlantic Ocean from 1985 to 1993. Feeding habits were examined in relation to larval stage. Metamorphic larvae were also collected as they entered an estuarine habitat in New Jersey, and their diet was examined.

Materials and methods

During fall and winter, pelagic larval summer flounder were collected in the NW Atlantic Ocean from 1985 to 1993 by the National Marine Fisheries Service (NMFS) Marine Resources Monitoring, Assessment, and Prediction (MARMAP) surveys (Able et al., 1990). These monthly to bimonthly surveys were conducted over the continental shelf from Cape Lookout, North Carolina, to Cape Sable, Nova Scotia, by the RV *Albatross IV* and the RV *Delaware II*. The vast majority (96.4%) of oceanic specimens were collected during October and November, and a few were collected in December, January, and March. Surveys used 61-cm diameter bongo frames fitted with 0.333- and 0.505-mm mesh nets (Sherman, 1980). The nets were towed obliquely through the water from the surface to depths of 22–75 m and back to the surface at a speed between 1.5 and 3.5 knots. Samples from 50 stations were the focus of this study (Fig. 1). Collections were chosen for analysis on the basis of number of summer flounder larvae that were present. All collections with 10 or more summer flounder larvae were examined. Additional stations with fewer specimens were examined to balance time blocks so that each 2-h block included at least 10 specimens and at least 2 collections, and to include the full size range of larvae.

Specimens were preserved in 10% formalin at sea and remained in formalin for approximately 12 months. They were then transferred to 70% ethanol. Specimen shrinkage clearly occurred as a result of fixation. Within 24 hours of examination specimens were soaked in glycerin where they remained throughout their dissection (see Arthur, 1976; Gadomski and Boehlert, 1984).

After standard length (SL) (snout to notochord tip until full flexion, then to posterior edge of hypurals, Gadomski and Boehlert, 1984) of each larva was measured and morphological stage was determined, the digestive tract was removed. Contents of the entire digestive tract were evaluated. Gut contents were teased out and prey items were identified to the lowest possible taxon.

Diet was analyzed in terms of numerical percentage composition (%N), volumetric percentage composition (%Vol), and percent frequency of occurrence (%FO). Prey that comprised <1% of the diet by number and by volume were pooled into the "other" prey category. Prey volumes were estimated, generally by assuming a spheroidal geometry, from prey dimensions. The three analyses (%N, %Vol, and %FO) were combined to yield a more comprehensive assessment

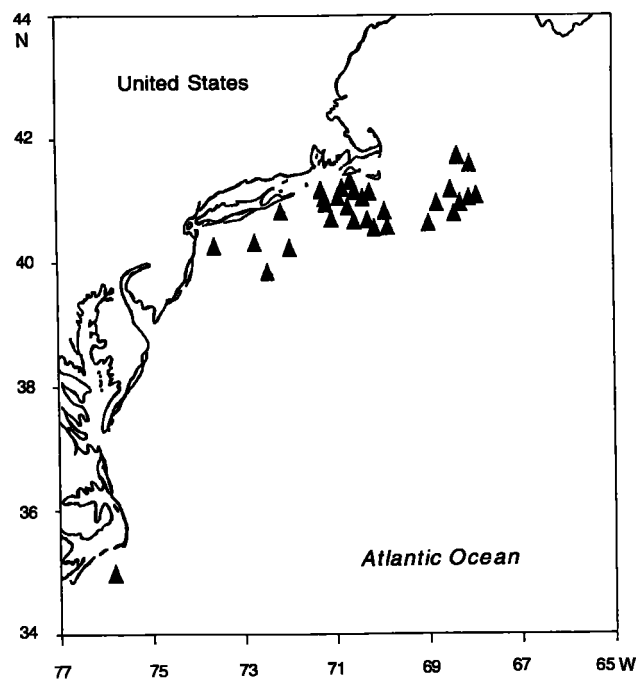


Figure 1

Location of the oceanic sites in the NW Atlantic Ocean, off the NE United States, where pelagic larval summer flounder, *P. dentatus*, were collected.

of prey importance, the index of relative importance (IRI = (%N + %Vol) × %FO) (Pinkas et al., 1971).

A comparison of larval sizes with established definitions of length at yolk absorption and length at flexion (Smith and Fahay, 1970; Martin and Drewry, 1978) revealed that considerable shrinkage had occurred prior to the examination of these specimens. As a result, data were pooled across stations for analysis by morphological stage, rather than by size class. Morphological stages were defined as preflexion (PF): straight notochord and no indication of caudal-fin ray development; flexion (FLX): beginning of caudal-fin ray development (i.e. ossification), accompanied or not by an upturn of the notochord tip and ossification of ural bones (hypurals, epurals, parhypurals); postflexion, premetamorph (PM): completion of caudal-fin ray ossification, upturn of notochord, and ossification of the ural bones, accompanied by resorption of the notochord tip, such that it no longer extends beyond the edge of the hypural bones (Fahay¹); and metamorph (M): metamorphic

¹ Fahay, M. 1995. Northeast Fisheries Science Center, Howard Marine Sciences Laboratory, Natl. Mar. Fish. Serv., NOAA, Highlands, NJ 07732. Personal commun.

stages F– through I (Keefe and Able, 1993), based on degree of eye migration.

Incidence of feeding and gut fullness were also examined, as a function of 2-h time blocks. Gut fullness (F) was recorded as 0 = empty, 1 = 1–25%, 2 = 26–50%, 3 = 51–75%, and 4 = 76–100% full. Incidence of feeding was recorded as the percent frequency of larvae that had prey in their guts (i.e. $F > 0$), in relation to the total number of specimens examined in a time block.

A total of 550 oceanic larvae were examined. Of these, 18 were excluded from analysis because large portions of their guts were missing, and 11 were excluded because their primitive condition likely impaired their ability to ingest prey (Blaxter, 1986; Gadomski²). Primitive characteristics included presence of yolk sac, absence of eye pigment, and undeveloped mouth. Evidence of prey ingestion was lacking in the 29 excluded larvae. This study was based on 521 oceanic larvae that were deemed to be functionally intact.

A second series of collections were examined to determine the feeding ecology of summer flounder larvae as they enter an estuarine nursery habitat. Metamorphic larvae were collected from plankton entering the Great Bay–Little Egg Harbor (New Jersey) estuary (Fig. 2) during fall, winter, and spring from 1989 to 1995. Most estuarine specimens (71.4%) were collected between November and January. The remainder were collected between February and June, and in October. Stationary plankton nets (1-m diameter, 1.0-mm mesh) were set for 30 min, at the surface and just off the bottom, on nocturnal flood tides, from a bridge across Little Sheepshead Creek (Szedlmayer et al., 1992; Keefe and Able, 1993). This site is characterized by Atlantic Ocean water on flood tides (Charlesworth, 1968, cited in Szedlmayer et al., 1992); thus larvae were likely captured as they entered the estuary from the ocean, or soon after.

Estuarine specimens were preserved in 95% ethanol, and they remained in ethanol until their examination. Specimens were processed as above. Because all estuarine specimens were metamorphic (ME), morphological stages were recorded in terms of Keefe and Able's (1993) metamorphic stages: F– through I. The estuarine portion of this study was based on 119 specimens.

Results

Preflexion (PF) larvae were the dominant morphological stage in oceanic collections, accounting for 84.3% of the specimens (Table 1). Later morphologi-

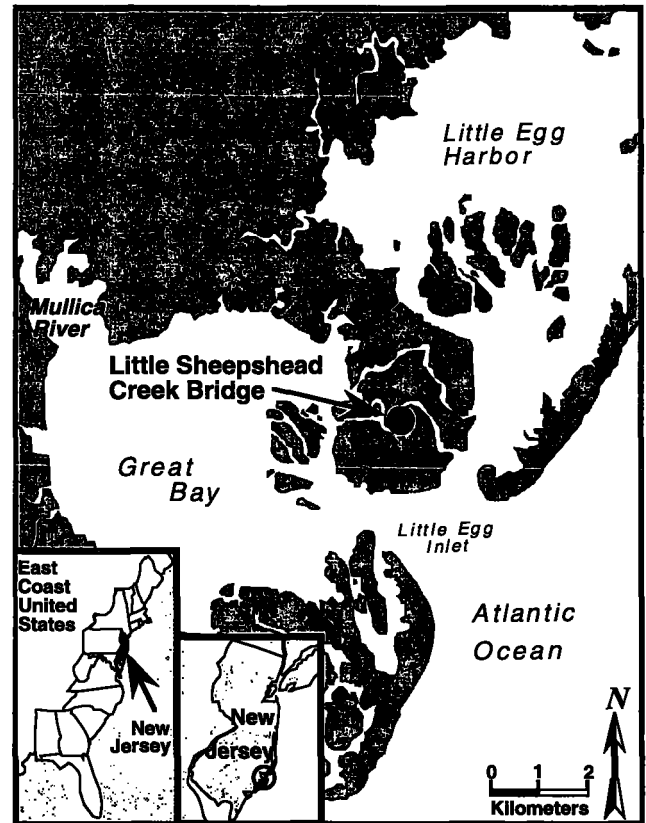


Figure 2

Location of the estuarine site in Little Sheepshead Creek, New Jersey, where metamorphic summer flounder, *P. dentatus*, were collected. (Figure by K. W. Able, Rutgers University.)

cal stages were progressively rarer, with flexion (FLX) larvae accounting for 12.5%, postflexion, premamorphic (PM) larvae accounting for 1.7%, and metamorphic (M) larvae accounting for 1.5% of the oceanic specimens in this study. Although greater than 33% of the larvae in each morphological stage contained prey in their guts, stages PM and M were combined for dietary analyses because of their small representation in these collections and similarity in diet.

Larval lengths that were recorded at the time samples were sorted (usually within 12 months of collection) were compared with lengths at the time of examination in order to estimate shrinkage. Comparisons based on 329 specimens defined mean shrinkage as 13.7% (SD=5.83).

Diet of reflexion (PF) larvae

The dominant stage in this study, PF, was represented by a total of 439 specimens: 56.9% contained recognizable prey, and 43.1% had empty guts. Lengths at the time of examination ranged from 1.9 to 6.9 mm SL (Table 1).

² Gadomski, D. 1995. Columbia River Research Laboratory, National Biological Service, 5501A Cook-Underwood Road, Cook, WA 98605. Personal commun.

Table 1

Feeding incidence and number of prey ingested by summer flounder, *P. dentatus*, larvae by time block, habitat, and larval stage. OC = oceanic, ES = estuarine, PF = preflexion, FLX = flexion, PM = premetamorphic, and M = metamorphic (oceanic). Estuarine metamorphic stages are as defined by Keefe and Able (1993). Numeric data exclude copepod eggs that appeared to have been ingested incidentally by metamorphic larvae.

	Habitat type	No. larvae examined	Standard length (mm)			No. larvae with food	Percentage feeding	Total no. food items	No. food items per feeding larvae
			mean	SD	range				
Time block (h)									
0000-0159	OC	67	3.8	1.22	2.3-7.5	11	16.4	40	3.6
	ES	15	11.4	1.29	8.6-13.4	1	6.7	1	1.0
0200-0359	OC	18	4.5	1.04	3.4-6.7	2	11.1	3	1.5
	ES	11	12.3	1.91	8.8-14.6	1	9.1	1	1.0
0400-0559	OC	60	4.8	1.35	2.2-7.2	5	8.3	7	1.4
	ES	11	11.3	0.97	9.5-12.9	2	18.2	3	1.5
0600-0759	OC	44	4.3	1.39	2.6-7.6	24	54.5	104	4.3
	ES	2	10.3	0.44	10.0-10.6	0	0.0	0	0.0
0800-0959	OC	10	4.1	0.76	3.2-5.3	10	100.0	46	4.6
1000-1159	OC	33	3.8	0.96	2.7-5.8	27	81.8	107	4.0
1200-1359	OC	39	3.7	1.23	2.1-8.0	38	97.4	259	6.8
1400-1559	OC	41	3.6	1.16	2.1-8.3	36	87.8	256	7.1
1600-1759	OC	67	3.6	0.70	2.6-6.2	47	70.1	168	3.6
1800-1959	OC	32	3.8	1.12	1.9-7.9	27	84.4	106	3.9
	ES	36	12.4	1.62	8.8-14.5	5	13.9	13	2.6
2000-2159	OC	60	3.9	1.37	2.3-9.0	42	70.0	258	6.1
	ES	39	11.9	1.48	8.1-13.9	5	12.8	12	2.4
2200-2359	OC	50	4.1	1.25	2.1-8.3	11	22.0	31	2.8
	ES	5	11.3	1.76	8.8-13.5	1	20.0	2	2.0
Larval stage									
PF	OC	439	3.6	0.85	1.9-6.9	250	56.9	1276	5.1
FLX	OC	65	5.6	0.75	3.7-7.2	22	33.8	86	3.9
PM	OC	9	6.6	0.92	4.8-7.6	4	44.4	17	4.3
M	OC	8	7.7	0.97	5.8-9.0	3	37.5	6	2.0
G	ES	47	11.9	1.74	8.1-14.4	9	19.1	19	2.1
H-	ES	34	12.0	1.51	8.8-14.6	3	8.8	7	2.3
H	ES	35	11.8	1.35	8.8-14.5	1	2.9	2	2.0
H+	ES	1	12.6		12.6	1	100.0	1	1.0
I	ES	2	13.3	0.71	12.8-13.8	1	50.0	3	3.0

Immature copepodites composed the bulk of the diet (61.4% Vol, 37.3% IRI; Table 2) of PF larvae. Copepod nauplii, the second most important prey, composed 20.0% (N and IRI) of the diet. Tintinnids, despite being the most abundantly ingested prey (28.7% N), ranked third in importance at 19.3% (IRI). Bivalve larvae and copepod eggs were the only other prey that accounted for >1% of the diet, and together they composed 21.7% (IRI).

The size of ingested prey was directly related to larval size. Only PF larvae, the smallest larvae, abundantly ingested small prey, i.e. tintinnids, copepod nauplii, copepod eggs, and bivalve larvae. Diatoms and dinoflagellates were also occasionally ingested (4.4% FO), although both were of such minor importance in the total diet that they were pooled into the "other" prey category. The mean number of prey

found in the guts of PF larvae was 5.1 (SD=4.47, range: 1-25). For PF larvae, the ingestion of copepod eggs and invertebrate eggs was clearly independent of the ingestion of berried females. Visual cues of prey may be important for feeding larvae because grains of sand that visually "mimicked" bivalve larvae, in size, shape, and color, were ingested along with bivalve larvae by 4.4% of PF larvae.

Diet of flexion (FLX) larvae

A total of 65 FLX specimens were represented in this study: 33.8% contained recognizable prey, and 66.2% had empty guts. Lengths at the time of examination ranged from 3.7 to 7.2 mm SL (Table 1).

Immature copepodites dominated the diet of FLX larvae, regardless of method of analysis (Table 3).

Table 2

Diet of pelagic preflexion (PF) summer flounder, *P. dentatus*, larvae collected from the NW Atlantic, in terms of numerical percentage composition (%N), volumetric percentage composition (%Vol), percentage frequency of occurrence (%FO), and percentage index of relative importance ($IRI = (\%N + \%Vol) \times \%FO$). All values are based on a sample size, with prey, of 250 larvae.

Prey	%N	%Vol	%FO	%IRI
Tintinnids	28.7	3.3	37.6	19.3
Copepod nauplii	20.0	10.2	41.2	20.0
Copepodites	16.0	61.4	30.0	37.3
Calanoids	0.6	4.9	2.0	0.2
Cyclopoids	0.6	2.0	2.4	0.1
Copepod eggs	16.0	1.2	34.8	9.6
Bivalve larvae	12.1	14.8	28.0	12.1
Invertebrate eggs	3.7	0.9	11.6	0.9
Other	2.3	1.3	9.2	0.5

The well-digested condition of copepodites precluded specific identifications, but most appeared to be calanoids. The only other prey category to represent more than 10% of the diet by any analysis was adult calanoid copepods, which despite accounting for 27.5% of dietary volume, composed only 6.0% IRI.

Tintinnids were not observed in the FLX larval diet, and other small prey items (copepod nauplii, copepod eggs, bivalve larvae, and invertebrate eggs) contributed little to the diet. The mean number of prey ingested by FLX larvae was 3.9 (SD=2.33, range=1-9).

Diet of oceanic premetamorphic and metamorphic (PM+M) larvae

A total of 9 PM and 8 M specimens were represented in this study: 44.4% of PM larvae and 37.5% of M larvae contained recognizable prey, and 55.6% of PM larvae and 62.5% of M larvae had empty guts. Lengths at the time of examination ranged from 4.8 to 7.6 mm SL for PM larvae and 5.8 to 9.0 mm SL for M larvae (Table 1). Combining the two stages (PM+M): 41.2% contained prey, and 58.8% had empty guts.

As with earlier morphological stages, immature copepodites were the primary prey for PM and M larvae, accounting for 50.1% of the diet (IRI). However, adult calanoid copepods and appendicularians, the secondary and tertiary prey (in terms of IRI), together contributed more than twice as much as copepodites to dietary volume (Table 4). Although it was not always possible to identify copepods to species, the most frequently ingested calanoid copepod

Table 3

Diet of pelagic flexion (FLX) summer flounder, *P. dentatus*, larvae collected from the NW Atlantic, in terms of numerical percentage composition (%N), volumetric percentage composition (%Vol), percentage frequency of occurrence (%FO), and percentage index of relative importance ($IRI = (\%N + \%Vol) \times \%FO$). All values are based on a sample size, with prey, of 22 larvae.

Prey	%N	%Vol	%FO	%IRI
Polychaete larvae	1.2	0.5	4.5	0.1
Copepod nauplii	2.3	0.2	9.1	0.2
Copepodites	68.6	66.7	86.4	92.8
Calanoids	13.9	27.5	18.2	6.0
Cyclopoids	3.5	1.9	9.1	0.4
Copepod eggs	3.5	<0.1	9.1	0.3
Bivalve larvae	5.8	2.8	4.5	0.3
Invertebrate eggs	1.2	0.4	4.5	0.1

Table 4

Diet of pelagic postflexion, premetamorphic (PM), and metamorphic (M) summer flounder, *P. dentatus*, larvae collected from the NW Atlantic, in terms of numerical percentage composition (%N), volumetric percentage composition (%Vol), percentage frequency of occurrence (%FO), and percentage index of relative importance ($IRI = (\%N + \%Vol) \times \%FO$). All values are based on a sample size, with prey, of 7 larvae. Data exclude copepod eggs that appeared to have been ingested incidentally.

Prey	%N	%Vol	%FO	%IRI
Copepod nauplii	8.7	0.5	28.6	1.7
Copepodites	60.9	27.1	42.9	50.1
Calanoids	13.0	34.6	42.9	27.2
Appendicularians	17.4	37.8	28.6	21.0

appeared to be *Centropages typicus*. *Temora longicornis* and *Pseudocalanus* spp. also contributed to the diet. Appendicularians were only observed in the diet of PM and M larvae.

The mean number of prey ingested by PM and M larvae was 3.3 (SD=2.14, range=1-6). Copepod eggs that were abundant in the gut of a single M-stage larva were excluded because they were probably ingested incidentally.

Incidence of feeding

An examination of incidence of feeding (defined as the percentage frequency of larvae with prey in their guts) in relation to 2-h time blocks over the course of

24 h (Table 1) revealed that pelagic larvae began feeding near sunrise in oceanic habitats. The presence of prey in larval guts reached its lowest point, 8.3%, at 0400–0559 hours, then dramatically increased to 54.5% at 0600–0759 hours, the time block of sunrise for all collections. The only time during which incidence of feeding was 100% was 0800–0959. Throughout hours of full daylight, incidence of feeding remained high, $\geq 70\%$. Late afternoon or early-evening feeding may have buoyed the feeding incidence at 2000–2159, but evidence of recent feeding decreased sharply from 2000–2159 to 2200–2359 hours. During late night hours, the percentage of larvae that had prey in their guts gradually decreased from 22.0% at 2200–2359 to 8.3% at 0400–0559.

Gut fullness

Because incidence of feeding data were generated from gut-fullness data (i.e. $F > 0$), they provide a qualitative measure of gut fullness; however, gut-fullness data also provide direct estimates of the volume of prey in the gut over the course of 24 h (Fig. 3). Although larvae appeared to begin feeding at 0600–0759, full guts were not observed until 1200–1359. Maximum gut fullness ($F=4$) was only seen at 1200–1559 and 2000–2159. The only time block during which all larvae contained prey in their guts was 0800–0959.

Diet of metamorphic (ME) larvae in estuaries

The estuarine portion of this study was based on 119 metamorphic larvae (ME), representing metamorphic stages G through I (Keefe and Able, 1993) (with $n=47$ at stage G, $n=34$ at stage H-, $n=35$ at stage H, $n=1$ at stage H+, and $n=2$ at stage I, Table 1). The guts of 15 (12.6%) ME larvae contained recognizable prey, and 87.4% had empty guts. At the time of examination, larval lengths ranged from 8.1 to 14.6 mm SL.

Pelagic feeding was clearly demonstrated by $> 85\%$ of ME larvae. The primary prey of pelagic ME larvae was the calanoid copepod *Temora longicornis*, regardless of the method of analysis (Table 5).

The mean number of prey found in the guts of ME larvae was 2.1 (SD=0.99, range=1–4). The relatively good condition of some prey items in the guts of fish collected late at night suggests that some prey were likely ingested after dark.

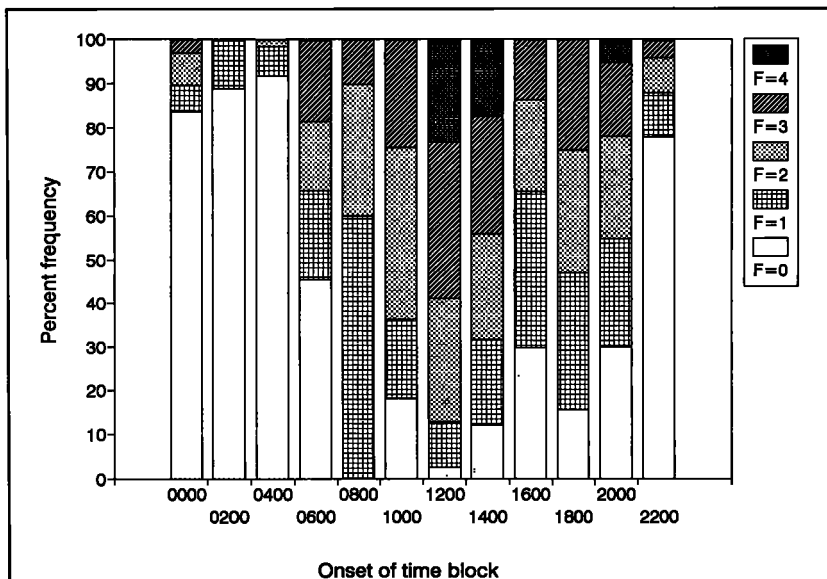


Figure 3

Gut fullness (F) of pelagic larval summer flounder *P. dentatus*, in the NW Atlantic Ocean, as a function of time of day (EST), where 0 = empty, 1 = 1–25%, 2 = 26–50%, 3 = 51–75%, and 4 = 76–100% full.

Table 5

Diet of metamorphic (ME) summer flounder, *P. dentatus*, larvae collected from a New Jersey estuary, in terms of numerical percentage composition (%N), volumetric percentage composition (%Vol), percentage frequency of occurrence (%FO), and percentage index of relative importance (IRI = (%N + %Vol) × %FO). All values are based on a sample size, with prey, of 15 larvae. Prey were pelagic unless otherwise indicated.

Prey	%N	%Vol	%FO	%IRI
Polychaete larvae	3.1	0.7	6.7	0.4
Polychaete tentacles (benthic)	3.1	12.0	6.7	1.6
Cirripede larvae	3.1	0.2	6.7	0.3
<i>Paracalanus parvus</i>	3.1	2.0	6.7	0.5
<i>Centropages typicus</i>	6.3	13.6	6.7	2.1
<i>Temora longicornis</i>	46.8	55.3	53.3	86.2
<i>Acartia</i> sp.	3.1	2.9	6.7	0.6
Unidentified calanoids	6.3	3.7	13.3	2.1
Harpacticoids (benthic)	6.3	1.5	6.7	0.8
Mysids (diurnal migrants)	9.4	6.1	13.3	3.3
<i>Oikopleura</i> sp.	6.3	1.8	13.3	1.7
Unidentified prey remnants	3.1	0.2	6.7	0.4

Evidence of benthic feeding was observed only in late-stage metamorphic larvae (H+ and I). Of two late-stage larvae that had prey in their guts, one

single larva (stage I, 13.8 mm SL) clearly demonstrated benthic feeding, having ingested polychaete tentacles and harpacticoid copepods, and the other larva had ingested a mysid, a taxon noted for diurnal migrations (Newell and Newell, 1977). All late-stage larvae in estuarine collections displayed noticeably darker pigmentation than was observed in earlier stages.

Incidence of feeding in estuaries

A comparison of the incidence of feeding of oceanic and estuarine summer flounder larvae was limited to nocturnal collections and revealed strikingly different patterns (Table 1; Fig. 4). Between 1800 and 0759 hours the incidence of feeding of estuarine larvae never exceeded 20.0%, whereas values for oceanic larvae ranged from 8.3% to 84.4%. The greatest differences between oceanic and estuarine larvae were observed early in the night: at 1800–1959 and 2000–2159 the incidence of feeding in estuarine collections was significantly lower than in oceanic collections ($P < 0.01$, $\chi^2 = 33.78$, 1 df, at 1800–1959; $P < 0.01$, $\chi^2 = 30.99$, 1 df, at 2000–2159) (Fig. 4). Because most (63.0%) larvae in estuarine samples were collected between 1800 and 2159 (Table 1), these comparisons were not biased by low sample size.

Within estuarine habitats, incidence of feeding declined with metamorphic stage, from 19.1% at stage G to 2.9% at stage H (Table 1). Time was not a factor in this decline because the distribution of larvae of stages G, H–, and H was the same across early-

(1800–2159), mid- (2200–0159), and late-night (0200–0559) collections ($P = 0.18$, $\chi^2 = 6.22$, 4 df).

Discussion

The diet of all stages of oceanic summer flounder larvae was dominated by immature copepodites in the NW Atlantic Ocean. The size of other ingested prey was directly related to larval size. Small prey items such as copepod nauplii, tintinnids, and bivalve larvae, were important only in the diet of early (PF) stage larvae. Large prey items, such as adult calanoid copepods and appendicularians were important only in the diet of later (PM and M) stage larvae.

The diet of metamorphosing (ME) larvae that were collected in a New Jersey estuary was dominated by the calanoid copepod *Temora longicornis*.

These observations differ sharply from the diet of metamorphosing larval summer flounder in a North Carolina estuary (Burke, 1995). Burke (1995) reported that the larval diet was dominated by polychaetes and mysids. However, all larvae in the North Carolina study (Burke, 1995) were caught in estuarine nursery areas with benthic trawls, whereas in the present study oceanic larvae were caught with bongo nets, and estuarine larvae were caught with stationary plankton nets. Clearly these two studies captured metamorphosing larvae during different ecological phases of the transition from pelagic to benthic ecology. The diet of late-stage metamorphic larvae that demonstrated benthic feeding in an estuarine habitat in the present study was similar to the diet of comparable size larvae in Burke's (1995) study. The darker pigmentation of benthic-feeding, late-stage larvae suggests that this pigmentation may be a valid marker of adaptation to the benthic habitat in summer flounder, as has been observed in other species (Grover et al., in press).

The pelagic diet of a congener, the olive flounder,³ *Paralichthys olivaceus*, may represent a more cogent comparison. In Wakasa Bay in the Japan Sea, Minami (1982) reported that

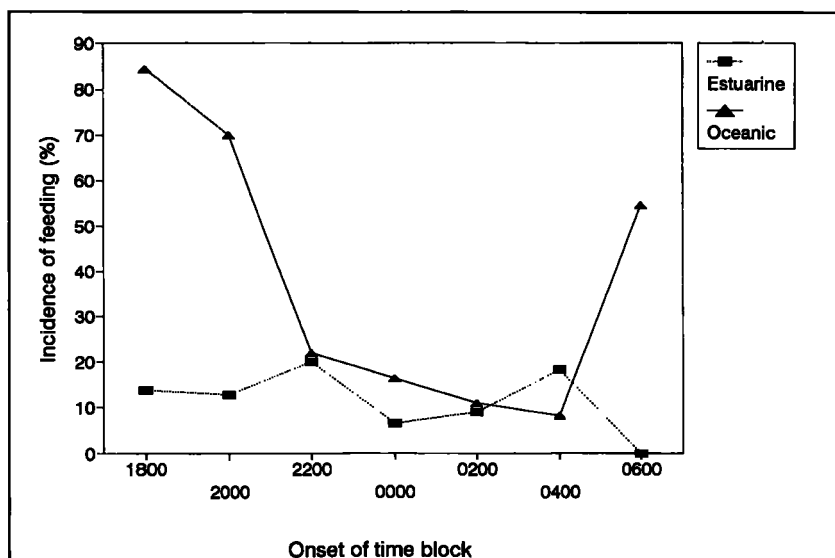


Figure 4

Incidence of feeding of larval summer flounder, *P. dentatus*, in the NW Atlantic Ocean and in a New Jersey estuary, as a function of time of day (EST) through the night. Data are based on a total of 331 oceanic and 119 estuarine specimens.

³ The common and scientific names of fish species used in *Fishery Bulletin* are those recommended by the American Fisheries Society (Am. Fish. Soc. Spec. Publ. 20, 5th ed., 1991). The following names have been changed accordingly: Japanese flounder to olive flounder; *Parophrys vetulus* to *Pleuronectes vetulus*; *Isopsetta isolepis* to *Pleuronectes isolepis*; and *Limanda ferruginea* to *Pleuronectes ferrugineus*.

copepod nauplii were the most important prey in the diet of all premetamorphic stages of Japanese flounder larvae. However, Ikewaki and Tanaka (1993) later reported that olive flounder diet, in Wakasa Bay, was dominated by copepod nauplii only for first-feeding larvae and by appendicularians, *Oikopleura* spp., for later stages through early-metamorphic-phase larvae. Minami (1982) reported that appendicularians, copepods, and mysids were the dominant prey of early-, mid-, and late-metamorphic larvae, respectively. The sizable contribution of copepod nauplii to the diet of preflexion (PF) summer flounder larvae resembled the contribution observed in the diet of first-feeding (Ikewaki and Tanaka, 1993) and early stage olive flounder larvae (Minami, 1982). However, appendicularians, the dominant prey item for early-metamorphic larvae (Minami, 1982), and for all larval stages beyond first-feeding in olive flounder (Ikewaki and Tanaka, 1993), occurred only in the diet of premetamorphic and metamorphic (PM+M) summer flounder larvae.

Pelagic summer flounder larvae that were collected in the NW Atlantic Ocean displayed a diurnal feeding pattern similar to that reported for several other flatfish larvae (e.g. plaice, *Pleuronectes platessa*: Shelbourne, 1953; Ryland, 1964; Last, 1978; dab, *Limanda limanda*: Last, 1978; English sole, *Pleuronectes vetulus*, and butter sole, *Pleuronectes isolepis*: Gadomski and Boehlert, 1984). Both incidence of feeding and gut-fullness data (Figs. 3 and 4) appear to confirm the visual nature of larval summer flounder feeding in oceanic collections. This is not surprising, because marine fish larvae are mostly visual feeders (Hunter, 1981; Blaxter, 1986; Huse, 1994). However, the optimal illumination level for feeding varies with species (Huse, 1994). For example, Atlantic cod, *Gadus morhua*, larvae feed preferentially at very low light levels, and turbot, *Scophthalmus maximus*, larvae feed preferentially at high levels of illumination, whereas plaice larvae feed over a wide range of illumination levels (Huse, 1994).

Within the flatfishes, additional relationships between illumination and larval feeding have been demonstrated. For example, sole, *Solea solea*, larvae can feed in the dark from the early posthatching stage (Blaxter, 1969). Oceanic collections of yellowtail flounder, *Pleuronectes ferrugineus*, larvae have shown that

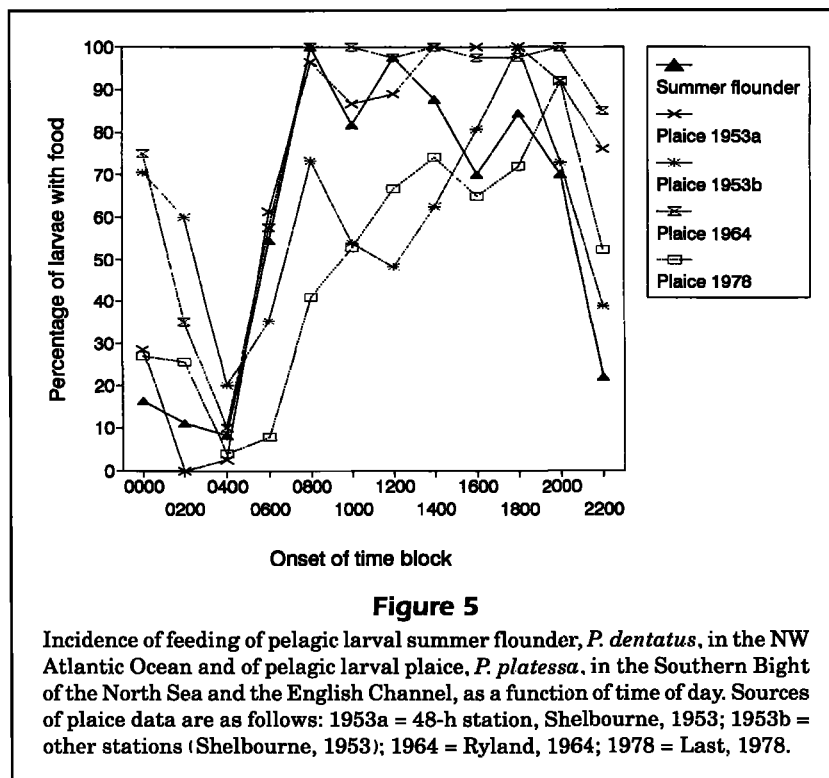


Figure 5

Incidence of feeding of pelagic larval summer flounder, *P. dentatus*, in the NW Atlantic Ocean and of pelagic larval plaice, *P. platessa*, in the Southern Bight of the North Sea and the English Channel, as a function of time of day. Sources of plaice data are as follows: 1953a = 48-h station, Shelbourne, 1953; 1953b = other stations (Shelbourne, 1953); 1964 = Ryland, 1964; 1978 = Last, 1978.

the highest incidence of feeding occurred between 1600 and 0100 (Smith et al., 1978). The near absence of feeding between 0700 and 1300 suggests that onset of feeding in yellowtail flounder larvae is triggered by something other than, or in addition to, illumination (Smith et al., 1978).

Data from oceanic collections in the present study suggest that the relationship between illumination and feeding of summer flounder larvae is much like that observed in one of the two flatfish species studied by Huse (1994). Laboratory observations are required to ascertain whether summer flounder larvae feed preferentially at high illumination levels or over a wide illumination range. However, an examination of incidence of feeding of pelagic plaice larvae (Shelbourne, 1953; Ryland, 1964; Last, 1978) in relation to comparable summer flounder data (Fig. 5) reveals similar patterns of feeding periodicity. From this, a similarity in optimal illumination levels for feeding for summer flounder and plaice larvae is suggested. To wit, pelagic summer flounder larvae would be expected to feed well over a wide range of illumination levels.

If the ecological analogy between plaice larvae and summer flounder larvae extends through metamorphosis, then a dramatic increase in light sensitivity (and a lower threshold light intensity for feeding) at metamorphosis (Blaxter, 1968) would be predicted for summer flounder. Limited field evidence supports this. A comparison of the incidence of feeding of oce-

anic and estuarine summer flounder larvae revealed strikingly different patterns (Fig. 4). Early in the night, incidence of feeding was much lower in estuarine collections. Fasting during metamorphosis, as has been noted in plaice (Riley, 1966; Lockwood 1984; Hamerlynck et al., 1989), may have contributed to this pattern. Plaice and sole have shown marked decreases in food-searching behaviors (distance covered per minute and time spent in feeding activity) at metamorphosis (Blaxter and Staines, 1971). Late at night, at 0400–0559, incidence of feeding in estuarine collections was double the rate seen in oceanic summer flounder collections (Fig. 4). A lower threshold light intensity for feeding at metamorphosis may have contributed to this, although small sample sizes of late-night estuarine collections preclude overreaching conclusions. Resolution of the threshold of light intensity for feeding of metamorphic summer flounder in a controlled laboratory setting could result in determination of optimal illumination levels at metamorphosis in aquaculture.

Metamorphosis has been considered a critical interval in the early life of some marine fishes (Thorisson, 1994). In the present study, the incidence of feeding of summer flounder larvae was observed to decline with metamorphic development to stage H. This suggests that the midpoint in the migration of the right eye (Keefe and Able, 1993) may be a critical period for summer flounder. In a laboratory study, a cessation of feeding was observed at stage G (Keefe and Able, 1993). However, cessation of feeding at metamorphosis may not place flatfish in any real danger of starvation (Lockwood, 1984). Metamorphic plaice larvae are capable of surviving without food for 7–25 d, without reaching the “point of no return” (Wyatt, 1972). Blaxter and Hempel (1963) have defined the “point of no return” as the point at which starved larvae become too weak to feed. Midmetamorphic summer flounder larvae are capable of surviving 56 d without reaching the “point of no return” (Keefe and Able, 1993). At metamorphosis and shortly thereafter flatfish may be more vulnerable to predation (van der Veer and Bergman, 1987; Witting and Able, 1993, 1995) than to starvation (Thorisson, 1994).

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