

Resource partitioning by *Menidia menidia* and *Menidia beryllina* (Osteichthyes: Atherinidae)

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ABSTRACT: Resource overlap values were calculated for habitat and food utilization by *Menidia menidia* and *M. beryllina* in 2 Rhode Island estuaries (USA). Habitat overlap was nearly complete during spring, but declined during summer and fall. Food overlap varied greatly throughout the year. The 2 species coexist because they: (a) overlap strongly in both food and habitat utilization only when food is abundant, and (b) have evolved different spawning times and different growth rates. *M. menidia* grows to a larger body size than *M. beryllina* and can utilize different habitats and foods when zooplankton becomes scarce. Time of hatching of each species in the upper estuary was related to cycles of zooplankton abundance. *M. menidia* larvae probably have a substantial predatory impact on zooplankton in the upper estuary during June of each year.

INTRODUCTION

Until recently, fishery ecologists studying competitive interactions concentrated on identifying species which used similar food or habitat resources (e.g. Nilsson, 1958; Gee and Northcote, 1963) with the hope of developing predictions of competitive exclusion. After Hardin (1960) pointed out that competitive exclusion hypotheses could not be falsified, a new body of ecological theory was developed, primarily by Levins (1968) and MacArthur (1972), which suggested ways in which sympatric species could partition resources to avoid competition. Schoener's (1974) extensive review of resource partitioning listed only 4 studies (Maitland, 1965; Keast, 1970; Zaret and Rand, 1971; Gibson, 1972) involving fish species. Since then, however, several investigators have demonstrated fish resource partitioning in both freshwater (Gascon and Leggett, 1977; Werner et al., 1977; George and Hadley, 1979; Smart and Gee, 1979) and coastal marine environments (Alevizon, 1975; McEachran and Musick, 1975; McEachran et al., 1976; Ross, 1977; MacPherson, 1981). Very few studies (Baker-Dittus, 1978; Clymer, 1978; Worgan and FitzGerald, 1981a; Prince et al., 1982; Thorman, 1982) have reported on resource partitioning by estuarine fish, even though an estuary, by its very nature, offers a diverse range of habitats and foods to be partitioned.

Ecologists have, in general, found resource partitioning among fish species whenever and wherever they

have looked for it. Alevizon (1975), Werner et al. (1977), Page and Schemske (1978), and Worgan and FitzGerald (1981a) all described partitioning of habitats when only habitats were examined. Keast (1977a, b), Baker-Dittus (1978), Desselle et al. (1978), Targett (1978), and Worgan and FitzGerald (1981b) described partitioning of food resources when only foods were examined. Ross (1977), Clymer (1978), Keast (1978), George and Hadley (1979), Smart and Gee (1979), Laughlin and Werner (1980) and MacPherson (1981) all showed that both food and habitats were partitioned simultaneously. Schoener (1974) noted that the most important resource dimension partitioned by groups of species was habitat in 55 % of the cases examined, food in 40 %, and time in 5 %. His literature review further showed that partitioning primarily along the resource dimension 'time of year' was an especially rare phenomenon. Rarity in this case may in part be due to the longer period of investigation required to demonstrate temporal partitioning. Many studies (especially those on vertebrates) have demonstrated food and habitat partitioning during only one season. In order to gain a fuller understanding of species interactions, however, it is sometimes necessary to follow species through several life stages. The partitioning of a resource by adults may simply be a result of partitioning of another resource by younger life stages during a previous season or year. Helfman (1978) has alluded to this problem in his discussion of coral reef fish community structure.

This paper reports on resource partitioning by the atherinid fish *Menidia menidia* and *M. beryllina* in 2 Rhode Island estuaries (USA). The 2 species studied are the only representatives of the fish family Atherinidae found in Rhode Island waters. The family consists primarily of small planktivores commonly present in estuaries, lagoons, and freshwater lakes around the world. The geographical range of *M. menidia* extends from the Gulf of St. Lawrence in Canada to northeastern Florida, USA, whereas *M. beryllina* has been reported from Cape Cod, USA, to Veracruz, Mexico (Johnson, 1975). Thus, they are sympatric in estuaries over much of the eastern coast of North America. A review of the literature on both species can be found in Bengtson (1982).

An attempt has been made to determine the basis of the partitioning by examining the full life histories of both species in relation to seasonal changes in the environment. Details of resource utilization by the 2 species are presented elsewhere (Bengtson, 1982), although resource overlap values calculated from those data are reported here. Resource overlap values are not used in this paper to indicate degree of competition between species. They simply indicate degree of similarity of resource utilization.

METHODS

This study was conducted in 2 estuaries, the Pettaquamscutt River and Point Judith Pond, located in southern Rhode Island, USA. Maps and descriptions of the estuaries were given by Bengtson (1982). On each estuary, 2 sampling stations were established, one near the mouth and one near the head, because previous literature (Hildebrand and Schroeder, 1928) suggested that the 2 species differed in salinity preferences. Fish were collected from April through November, 1976, by beach seine (30 m long, 6.3 mm mesh) in 3 standard quadrats (23 by 30 m) established at each station. Members of each species were identified and enumerated, and the data (numbers of fish m^{-2}) were presented by Bengtson (1982). From those data, I have here calculated resource overlap values (α_{ij}) for habitat overlap according to the formula of Levins (1968):

$$\alpha_{ij} = \frac{\sum P_{ih} P_{jh}}{\sum P_{ih}^2} \quad (1)$$

where P_{ih} = proportion of utilization of resource h by species i ; P_{jh} = proportion of utilization of resource h by species j . Resource overlap (α_{ij}) represents the overlap of the resource usage of species j on that of species i relative to the total resource utilization of species i and values vary from 0 to slightly greater than 1. Of the fish collected at each station on each sampling date, a

subsample of 10 members (> 20 mm SL) of each species (if available) was selected for analysis of gut contents. Specific data on the gut contents given by Bengtson (1982) provide the basis for resource overlap values (α_{ij}) for food reported here. Food resource overlap was based on the fishes' consumption of several food types as given by Bengtson (1982), whereas habitat resource overlap was based on utilization of only two habitats, upper and lower estuary.

Sampling was also conducted at the same stations with a 3.2 mm mesh seine net (3 m long) in 1976. Standard lengths of the fish preserved (10 % formalin) from each collection were subsequently measured in the laboratory.

Daily measurements of temperature, salinity, and zooplankton abundance were made during 1977–1979 at a site in the upper Pettaquamscutt River. Specifically, sampling was conducted 5 d wk^{-1} between 0630 and 0730 from May–December, 1977, and May–November, 1978, and 3 d wk^{-1} from April–October, 1979, coincident with the growing season of young-of-the-year (YOY) fish of both species. The upper river was usually covered with ice from December–March. Zooplankton sampling was conducted from a dock adjacent to one of the fish sampling quadrats in water slightly greater than 1 m in depth. Surface temperature and salinity were measured with thermometer and hydrometer, respectively, and 3 vertical plankton tows of 0.91 m depth were made with a 0.30 m diameter, 1.14 m long, 0.080 mm mesh plankton net. Samples were returned to the laboratory, reduced to 50 ml volume, mixed thoroughly, and the organisms in 3 1-ml subsamples of each sample counted. In 1978 and 1979, the remainder of each sample was dried at 60°C for 48 h for determination of biomass.

RESULTS

Habitat overlap values for both estuaries (Table 1) indicate that *Menidia menidia* and *M. beryllina* were almost identical in their habitat usage during spring. At that time, both species occupied the upper ends of both estuaries almost exclusively. In summer, overlap values generally declined, reflecting the fact that some *M. menidia* moved to the lower portion of the estuary while other *M. menidia* and almost all of the *M. beryllina* remained in the upper portion. Overlap of *M. menidia* on *M. beryllina* was usually greater than that of *M. beryllina* on *M. menidia*, because *M. beryllina* was restricted to one habitat (upper estuary) while *M. menidia* occupied both habitats (upper and lower estuary). During the latter part of the summer, year class 0 *M. beryllina* were not collected because they were usually too small to be retained by the net mesh, so

Table 1. Habitat overlap values (Levins' α) for *Menidia menidia* and *M. beryllina* in Pettaquamscutt River (PR) and Point Judith Pond (PJP) on sampling dates in 1976. For each estuary on each date, the upper value is the overlap of *M. beryllina* on *M. menidia*, the lower value that of *M. menidia* on *M. beryllina*. Dashes: either an estuary was not sampled or one species was totally lacking from all collections on that date

Location	Date							
	5/26	6/3	6/16	7/2	7/13	4/8	4/22	5/6
PR	1.01	1.13	1.01	1.00	1.02	1.05	0.47	0.63
	0.99	0.87	0.99	1.00	0.98	0.96	0.34	0.99
PJP	1.19	0.94	0.95	1.06	1.06	1.08	1.02	1.08
	0.65	1.06	1.05	0.94	0.94	0.92	0.97	0.61

Location	Date							
	7/28	8/13	8/31	9/26	10/11	10/24	11/6	11/20
PR	0.96	0.63	1.10	-	0.89	0.02	0.13	0.38
	0.98	0.33	0.84	-	0.87	0.02	0.16	0.24
PJP	0.00	-	1.20	1.19	1.20	0.03	0.01	0.00
	0.00	-	0.74	0.65	0.77	0.03	0.01	0.00

overlap values could not be calculated. During autumn, year class 0 *M. beryllina* were collected regularly in the upper portions of both estuaries, although in early October they were present in both upper and lower estuary. Overlap values after mid-October were generally the lowest of the year and indicate the nearly complete separation of the species (*M. beryllina* in the upper estuary, *M. menidia* in the lower) at that time. Thus, the 2 species occupied the upper estuary from spring until early fall, but only *M. menidia* occupied the lower estuary in significant numbers from July to November. This pattern was confirmed by data from the second year of sampling in 1977 (Bengtson, 1982).

Food overlap values (Table 2) are given for fish from the upper estuary stations only because *Menidia beryllina* were rarely collected in sufficient numbers for analysis at the lower estuary stations, and almost all the overlap in habitat between *M. menidia* and *M. beryllina* occurred at the upper estuary stations (Bengtson, 1982). Food overlap values were calculated only for fish at one station at a time rather than between stations, because diets of fish at the different stations varied considerably depending on the food available (Bengtson, 1982). Food overlap values varied substantially throughout the year and consistent seasonal trends were not clearly apparent. Generally, diet overlap was high during spring when zooplankton food was more abundant (Fig. 3 to 5), although there were exceptions to that generality. During summer, diet overlap was low in the upper Pettaquamscutt River, but high in Point Judith Pond. Overlap increased again during the fall in the Pettaquamscutt River. Perhaps

Table 2. Food overlap values (Levins' α) for *Menidia menidia* and *M. beryllina* in the upper Pettaquamscutt River (UPR) and upper Point Judith Pond (UPJP) on sampling dates in 1976. For each estuary on each date, the upper value is the overlap of *M. beryllina* on *M. menidia*, the lower value that of *M. menidia* on *M. beryllina*. Dashes: fewer than 10 members of a species collected on a particular date were available for analysis

Location	Date						
	4/8	4/22	5/6	5/26	6/3	6/16	7/2
UPR	0.87	0.25	-	0.60	0.37	1.32	0.03
	0.59	0.33	-	0.95	0.52	0.68	0.02
UPJP	0.93	0.98	0.74	0.31	0.89	0.88	0.09
	1.07	1.02	1.28	0.21	1.06	1.12	0.17

Location	Date						
	8/31	9/18	9/26	10/11	10/24	11/6	11/20
UPR	0.03	0.05	0.52	1.09	0.43	1.05	1.00
	0.02	0.08	0.89	0.87	0.26	0.95	1.00
UPJP	1.03	0.92	0.01	0.57	1.13	-	-
	0.69	1.08	0.02	0.76	0.80	-	-

the most important point to be garnered from the data in Table 2 is that *M. menidia* and *M. beryllina* were capable of exhibiting pronounced dietary overlap in any season of the year when they occupied the same habitat.

A graph of mean (\pm standard deviation) standard length of each species from all sampling stations on each sampling date (Fig. 1) suggests the mechanism by which the 2 species are able to coexist. Body sizes of the two never overlapped; and, for a particular year class, *Menidia menidia* was always larger than *M. beryllina*. An examination of the set of mean standard lengths of year class 0 fish of each species shows that *M. menidia* hatched earlier and grew at a faster rate than year class 0 *M. beryllina*. That *M. menidia* spawn earlier was demonstrated by the fact that gravid *M. menidia* were collected from late April to early July, whereas gravid *M. beryllina* were collected only in June and July. Year class 0 *M. menidia* grew most rapidly during summer; growth rate subsequently declined during fall and winter. Year class I *M. menidia* continued to grow in length during the spawning season (April-July) and again during summer after spawning. They gradually declined in abundance during summer and fall after spawning and finally disappeared in late fall. Year class 0 *M. beryllina* evidently grow rapidly immediately after hatching in June, attaining a length of 20 mm in July. Eggs hatched in the laboratory yielded larvae of 3 to 4 mm total length. Growth rate of year class 0 *M. beryllina* during most of the summer and fall, however, is much

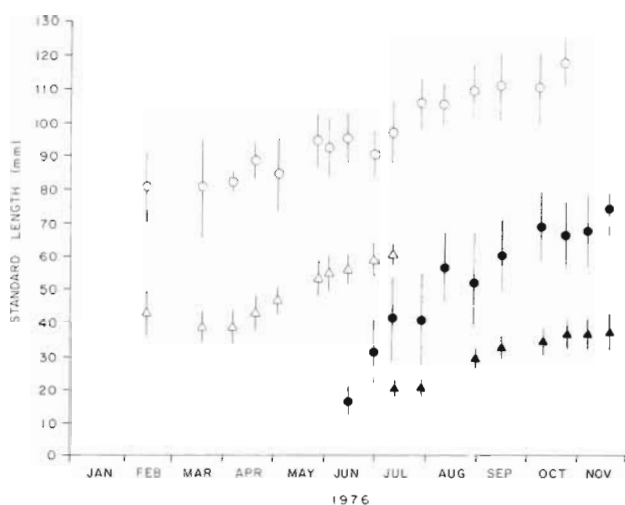


Fig. 1. *Menidia menidia* and *M. beryllina*. Mean (\pm standard deviation) standard lengths on sampling dates in 1976. Data are for fish from both upper and lower estuary sampling stations on both the Pettaquamscutt River and Point Judith Pond estuaries. Open circle: *M. menidia* year class I; closed circle: *M. menidia* year class 0; open triangle: *M. beryllina* year class I; closed triangle: *M. beryllina* year class 0. N for each year class of each species on each date varies from 14 to 653

less than that of year class 0 *M. menidia*. The lengths of *M. beryllina* collected in March and April suggest that very little growth occurred during the winter. Beginning in late April, *M. beryllina* exhibited a spurt of growth that continued into July (i.e. growth of both somatic and gonadal tissues occurred simultaneously). Unlike *M. menidia* adults, *M. beryllina* adults did not continue to grow during summer and fall after spawning. Had the *M. beryllina* continued to abound and grow, their mean body size would have overlapped with that of year class 0 *M. menidia*. The potential overlap in body size of year class 0 *M. menidia* and year class I *M. beryllina* during August would have been the only overlap that occurred during the life histories of the 2 species. The fact that such overlap did not occur because of the disappearance of *M. beryllina* adults suggests that strong competition may have occurred between the two. *M. beryllina* have been maintained in laboratory culture for nearly 2 yr (own obs.) although they have not spawned.

As a result of the observations that the greatest habitat overlap between the 2 species occurred in the upper Pettaquamscutt River and that *Menidia menidia* adults spawned earlier and juveniles grew faster than did *M. beryllina* adults and juveniles, an analysis of daily changes in certain environmental variables in the upper river was conducted from 1977 to 1979. Temperature and salinity fluctuations followed a fairly consistent pattern from year to year (Fig. 2). Temperature reached a yearly maximum in July or August of

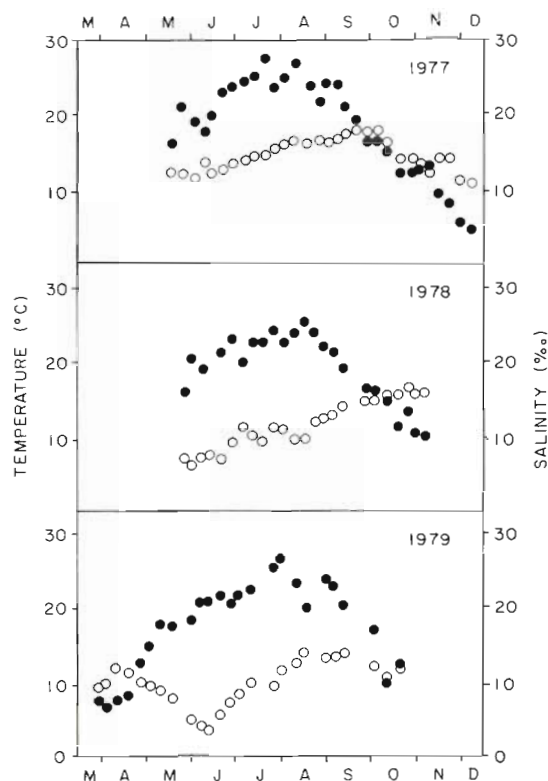


Fig. 2. Weekly means of morning temperature and salinity in the upper Pettaquamscutt River from spring to fall, 1977–79. Each data point for 1977 and 1978 represents the mean of 5 daily measurements. Each data point for 1979 represents the mean of 3 daily measurements. Closed circles: temperature; open circles: salinity

each year and declined rapidly in the autumn. Salinity increased slowly from a minimum in May–June to a maximum in September–October, reflecting the typical Rhode Island weather pattern of more abundant rainfall in spring than in late summer.

Zooplankton in the upper river also exhibited consistent patterns from year to year (Fig. 3 to 5). In 1977 (Fig. 3), only numerical abundance of zooplankton was measured. Zooplankton abundance gradually declined from mid-May until late June, rose to a peak in early July, declined again, reached a second peak in late August, and declined sharply in September. Abundance in May was due primarily to the copepods *Eurytemora affinis* and *Acartia tonsa* as well as barnacle nauplii, abundance in July to *A. tonsa* copepodites and adults, and abundance in August to several species of copepod nauplii. The ctenophore *Mnemiopsis leidyi* was abundant (although not included in zooplankton abundance counts) in the upper river beginning in late July.

In 1978 (Fig. 4), there was again a decline in zooplankton numerical abundance from mid-May through late June, although zooplankton biomass peaked in

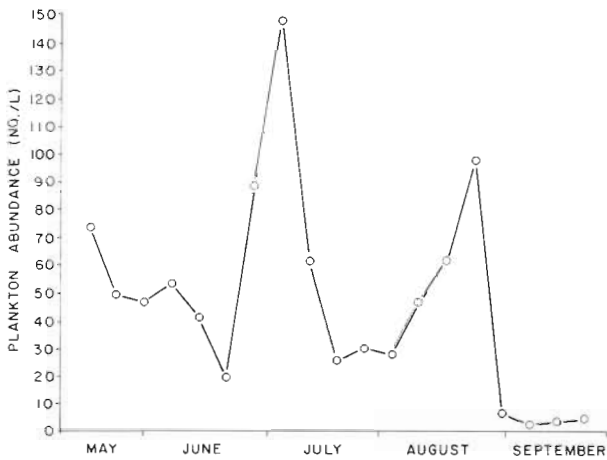


Fig. 3. Weekly averages of zooplankton abundance (number of organisms l^{-1}) in the littoral zone of the upper Pettaquamscutt River in 1977. Each data point represents the mean of 15 samples ($3 \text{ samples } d^{-1}, 5 \text{ d } wk^{-1}$)

early June. A lesser peak of both numerical abundance and biomass occurred in late July, followed by a decline in biomass, but an increase in numerical abundance. Once again, the May–June peak was due to copepods and barnacle nauplii, the July peak to *Acartia tonsa* copepodites and adults, and the August peak in numerical abundance to copepod nauplii. Ctenophores were abundant from early August through September.

In 1979 (Fig. 5), sampling began in early April to obtain a more complete picture of the yearly zooplankton cycle. Maximum biomass occurred in April, after which there was a gradual decline (except for a minor peak in mid-May) until early June. Numerical abun-

dance peaked in July, then declined from August on. The spring peak was again due primarily to *Acartia tonsa* and *Eurytemora affinis* copepodites and adults and to barnacle nauplii. The numerical abundance maximum in early July resulted from a bloom of rotifers, but the late-July peak in biomass was due to *A. tonsa* copepodites and adults. No pronounced peak of nauplii was observed in August, however. Ctenophores again became abundant in late July of 1979.

In summary, the typical zooplankton pattern observed during 1977–1979 was: a peak of barnacle nauplii and copepods in spring, a relative minimum sometime in June, a second copepod peak in July, followed by a sharp decline in biomass in August that lasted into autumn. Thus, in spring, when *Menidia menidia* adults become gravid, spawn, and larvae begin to hatch, zooplankton is abundant (although declining) and temperatures are increasing. In June, when most *M. menidia* larvae have hatched, zooplankton abundance is at a minimum and temperature continues to increase. In July, when year class 0 *M. menidia* and *M. beryllina* grow rapidly, zooplankton is very abundant and temperatures are at or near the yearly maximum. Finally, in late summer and autumn, when zooplankton abundance declines markedly and temperatures also decrease, growth rates of juveniles of both species decline also.

DISCUSSION

Coexistence of *Menidia menidia* and *M. beryllina* in the northern portion of the range of both species

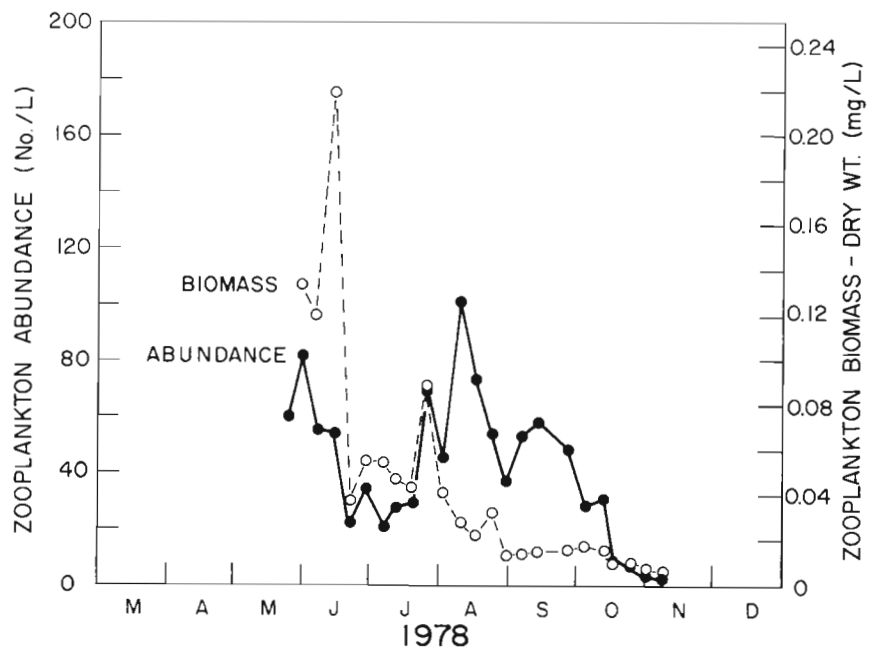


Fig. 4. Weekly averages of zooplankton numerical abundance (number of organisms l^{-1}) (solid line) and dry weight biomass ($mg\ l^{-1}$) (dashed line) in the littoral zone of the upper Pettaquamscutt River in 1978. Each data point represents the mean of 15 samples ($3 \text{ samples } d^{-1}, 5 \text{ d } wk^{-1}$)

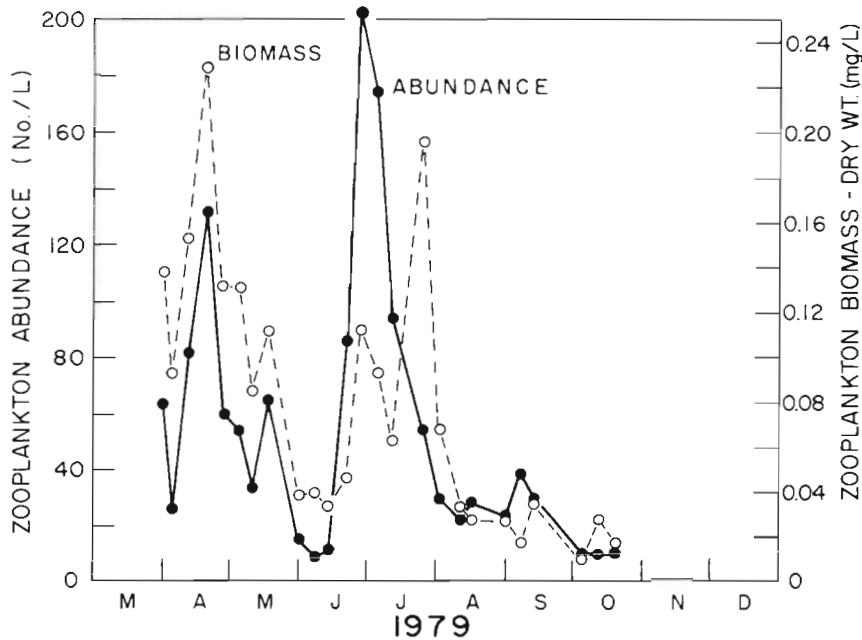


Fig. 5. Weekly averages of zooplankton numerical abundance (number of organisms l^{-1}) (solid line) and dry weight biomass ($mg\ l^{-1}$) (dashed line) in the littoral zone of the upper Pettaquamscutt River in 1979. Each data point represents the mean of 9 samples (3 samples d^{-1} , 3 $d\ wk^{-1}$)

appears to be made possible by 2 factors: (a) abundant food during the spring; (b) faster growth of *M. menidia* that enables them to move to a different (lower estuary) habitat in summer and fall. Habitat and food overlap values were typically high (values > 0.7 indicate a high degree of overlap: Keast, 1978) in spring, but values were occasionally high at other times of year as well. The congruence of high values for food and habitat overlap during the spring period of abundant zooplankton (Fig. 5) indicates that adults of the 2 species are able to coexist for short periods when food is abundant. The lower values for both food and habitat overlap for year class 0 fish during summer and fall suggest that juveniles of the 2 species partitioned resources more than adults. That is noteworthy in view of the fact that zooplankton abundance declined at those times (Fig. 3 to 5). The larger size of juvenile *M. menidia* during summer and fall apparently enabled some of them to occupy the lower estuary and to feed on benthic macroinvertebrates and larval fish during times of zooplankton scarcity (Bengtson, 1982). The search for an answer to the problem of coexistence then requires an examination of the early life history of the two species with regard to times of hatching and growth rates.

Mulkana's (1966) length-frequency diagrams indicated that juvenile *Menidia menidia* grew very rapidly in the summer months in Rhode Island. Because *M. menidia* spawn from late April to early July, however, his estimates of mean length of juvenile *M. menidia* collected during summer had a large variance, and his growth rate estimates (about $0.5\ mm\ d^{-1}$) were too low because of the continuous addition of new recruits to the population. Recently, Barkman et al. (1981) used

otolith daily growth rings to develop a much more precise age-length relation for juvenile *M. menidia* which yielded a growth rate estimate of $0.84\ mm\ d^{-1}$ for wild fish during the summer growing season. Furthermore, they found that *M. menidia* which hatched earlier in the season were longer at any given age than those that hatched later in the season. Thus, an early-hatched fish at age 40 d would be 40.1 mm in length, whereas a later-hatched fish at age 40 d would be only 36.8 mm long. Those results are particularly surprising in view of the fact that water temperatures are warmer during the early life of a late-hatched fish than during the early life of an early-hatched fish. Bengtson and Barkman (1981) found that growth of *M. menidia* increased with increased water temperature when food supply is held constant. Other explanations for the larger size of early-hatched fish may be larger size at hatching or a more abundant food supply.

In contrast to *Menidia menidia*, *M. beryllina* spawn during a relatively short time period in June and July. Lengths of young-of-the-year (YOY) fish, therefore, tend to vary less than lengths of *M. menidia* YOY fish. Accurate estimates of growth rates of YOY *M. beryllina* are obtainable from length-time data such as those presented in Fig. 1. The estimate for growth rate of *M. beryllina* beginning at 20 mm total length (because those were the smallest collected) and measured for the next 74 d period (for comparison with data of Barkman et al., 1981) is about $0.19\ mm\ d^{-1}$. That finding, taken with the observation of Barkman et al. that early-hatched *M. menidia* grow faster than late-hatched *M. menidia*, suggests a trend; to wit, the later an atherinid fish is spawned (in Rhode Island waters), the slower its growth rate will be.

The timing of *Menidia* larval abundance with cycles of zooplankton abundance is intriguing. Hatching of *M. menidia* larvae in the upper Pettaquamscutt River peaks in late May to early June (Barkman et al., 1981), during the latter part of the period of spring zooplankton abundance. Zooplankton abundance declined following the appearance of *M. menidia* each year. The 2 phenomena would appear to be related. In years (1977, 1978) in which *M. menidia* postlarvae were first collected in early June (Bengtson, 1982), the zooplankton decline occurred in late June. In the year (1979) in which *M. menidia* postlarvae were collected in mid-May (Bengtson, 1982), the zooplankton decline occurred in early June. In each year, the July zooplankton peak coincided with the hatching and early growth of *M. beryllina*. These data suggest that *M. menidia* and *M. beryllina* have evolved larval hatching times synchronous with periods of abundant zooplankton. This strategy has been documented for sardine and anchovy in the Adriatic (Vucetic, 1975).

Although the August zooplankton decline may be due to predation by ctenophores, similar to the phenomenon described by Hulsizer (1976) for the adjacent Narragansett Bay, the June zooplankton decline in the upper Pettaquamscutt River can be attributed to predation by *Menidia menidia*. Using a density estimate of 25 postlarval *M. menidia* m^{-3} , an average wet weight per fish of 4 mg (for postlarval fish of 11 to 12 mm TL), a consumption rate of 400 % of wet fish body weight in wet weight of food per day (all estimates from data of Bengtson, 1982), and the appropriate wet weight: dry weight conversions, one calculates that the *M. menidia* postlarvae consume 40 mg dry weight of food $m^{-3} d^{-1}$. Thus, (with reference to Fig. 4 and 5) they are capable of cropping the zooplankton peak abundance in one week's time and the amount of zooplankton available during periods of low abundance in June was insufficient to satisfy their needs for even one day. Hence, I conclude that food is a limiting resource in the upper Pettaquamscutt in the sense that all *M. menidia* postlarvae are not able to obtain the food they require to achieve maximum growth rates.

If *Menidia menidia* are in fact largely responsible for the June zooplankton decline and true differences in growth exist between early- and late-hatched fish, then an advantage accrues to the former. They hatch at a time when food is more abundant and undergo rapid growth so that they are less susceptible to predation (Cushing and Harris, 1973) and can ingest a larger range of prey items if zooplankton abundance declines. They are also able to feed on the abundant zooplankton available in July in addition to the spring zooplankton bloom. Barkman et al. (1981) found that early-hatched *M. menidia* remain in the upper Pettaquamscutt for only about 50 days, after which they

presumably move downriver (Bengtson, 1982). Their ability to enter the lower river, with its more abundant predators (Mulkana, 1966), enables them to feed on epibenthic prey in and around eelgrass (*Zostera*) beds when zooplankton abundance declines in late summer and fall (Bengtson, 1982). Large size would be a further advantage in late fall and winter when *M. menidia* moves into deeper, offshore waters (Richards and Castagna, 1970; Conover and Murawski, 1982). Judging by the emaciated appearance of Atlantic silversides when they return to the estuary in spring, the fish probably metabolize their body tissues during the winter.

Menidia beryllina hatches in July during a period of abundant zooplankton food, but does not consume as much as *M. menidia* and is not as abundant as *M. menidia* (Bengtson, 1982). Therefore, *M. beryllina* is not likely to account for the August decline in zooplankton abundance. Using an analysis like that given above for food consumption by *M. menidia* and assuming a density of 5 *M. beryllina* m^{-3} , weight of 4 mg fish $^{-1}$, and consumption of 150 % of body weight d^{-1} (all estimates from data of Bengtson, 1982), one calculates that *M. beryllina* is capable of consuming only 3 mg dry weight of food $m^{-3} d^{-1}$. Rather, ctenophores are major predators on zooplankton in Rhode Island waters at this time of year (Hulsizer, 1976; Kremer, 1979). In the upper Pettaquamscutt from August through the autumn in each year, the most abundant zooplankters were copepod nauplii and biomass was often less than 20 mg m^{-3} . By August, *M. beryllina* did not grow to a size that enabled them to feed on other non-zooplankton foods when zooplankton abundance declined, so from August onward they had to rely for food on the sparse zooplankton that was available. They showed a tendency to move to the lower estuary only in October (Bengtson, 1982) after the majority of predators had departed. The July hatching time of *M. beryllina* essentially places them in competition for food with the ctenophore *Mnemiopsis leidyi*. The scarcity of food insures that the *M. beryllina* grow slowly during the late summer and fall and, in fact, they do not exhibit a spurt in somatic growth until the following spring zooplankton bloom (Fig. 1).

There is latitudinal variation in the spawning time of *Menidia menidia* and *M. beryllina*. Spawning begins in South Carolina during March (Middaugh and Lempeis, 1976; Middaugh, 1981), Chesapeake Bay during April (Bayliff, 1950), Massachusetts during May (Bigelow and Schroeder, 1953; Conover and Ross, 1982), and Nova Scotia during June (Daborn et al., 1979). *M. beryllina* spawns in April in the Chesapeake (Hildebrand and Schroeder, 1928), and in June in Rhode Island (Bengtson, 1982) and at Woods Hole, Massachusetts (Sumner et al., 1913; Bigelow and

Schroeder, 1953). Similarly, latitudinal variation in the timing of the ctenophore, *Mnemiopsis leidyi*, bloom also exists. They are abundant in April, May, and June in North Carolina (Miller, 1974), June and July in Virginia (Burrell, 1968), June through October in Maryland (Herman et al., 1968), and July through October in Rhode Island (Kremer and Nixon, 1976). Thus, along the east coast of the United States, *M. beryllina* larvae probably appear temporally intermediate between 2 important consumers of zooplankton, *M. menidia* and *M. leidyi*. The ability of *M. beryllina* to exist along the east coast is at least in part a result of adaptation to competition with those species. Experiments on competition between *M. menidia* and *M. beryllina* (Bengtson, 1982) indicated that, if natural hatching times were separated by only 1 wk, rather than approximately 1 mo, *M. menidia* would have a strong competitive advantage against *M. beryllina* because of *M. menidia*'s ability to consume larger amounts of food. Presumably, if *M. beryllina* were to spawn after *M. menidia* north of Cape Cod, they would have to do so in July (because *M. menidia* spawns in June) and larvae might not hatch until August, which would allow very little time for significant growth before the onset of cold temperatures.

The phenomenon of temporal differences in the appearance of larvae has been described for several freshwater fish species in temperate waters. Gibbons and Gee (1972) found that longnose dace *Rhinichthys cataractae* spawned earlier than blacknose dace *Rhinichthys atratulus*, with the result that larvae of the 2 species occupied the same habitat at different times. Whether *R. cataractae* attained greater length at the end of the first summer because of the earlier spawning time was not reported in the paper, but the authors did state that *R. cataractae* attained sexual maturity at age 2, whereas *R. atratulus* required 3 yr to mature. Amundrud et al. (1974) and Keast (1980) described the sequential appearance of larvae of 6 centrarchid and percid species in an Ontario (Canada) lake and further demonstrated the decline in numbers of certain zooplankters coincident with the appearance of the fish larvae. Whether size at the end of the first growing season was correlated with time of appearance of larvae was again not reported. However, an examination of data on lengths of age class 0 fish of 4 of the 6 species in the same lake (Keast 1977a, b, 1978, 1980) indicates that the earlier in the year a species hatched, the larger it grew during the first summer.

Spawning time and potential growth rate for a particular species are determined over evolutionary time and it seems that a relation exists between the 2 for some temperate fish populations. Further investigation of this relation could help to elucidate the importance of larval fish ecology to resource partitioning by adults,

as suggested by Helfman (1978). Consideration of all life history stages may demonstrate that temporal partitioning of resources is more important than Schoener's (1974) study indicated.

The partitioning of resources by *Menidia menidia* and *M. beryllina* in Rhode Island waters depends ultimately on a temporal partitioning of the habitat and foods of the upper estuary, particularly by larvae. Partitioning of habitat by juveniles and adults varies substantially throughout the year, with more partitioning apparent in the summer and fall than in the spring, when food may not be limiting. Partitioning of food often reflected partitioning of habitat and, hence, also varied greatly. Both food and habitat partitioning are effected by the larger body size of *M. menidia* which, in turn, is brought about by its earlier spawning time and faster growth rates.

This study concludes that coexistence of 2 *Menidia* species in Rhode Island estuaries is achieved by the circumvention of competition by means of resource partitioning. No attempt was made to determine whether coexistence might be mediated by predation rather than competition. My observations in the field indicate that these species were subject to predation by both fish and birds. Nevertheless, I considered that accurate measurement of the effect of predation on coexistence approached the realm of impossibility and was at least beyond the scope of this study. The importance of competition in determining the mechanisms for coexistence of the two species is borne out by laboratory competition experiments using postlarvae, described elsewhere (Bengtson, 1982). Also, the virtual disappearance of *M. beryllina* adults shortly after spawning, at the one time of the year when their continued existence would lead to overlap in body size with juvenile *M. menidia* suggests that competition may be strong. If laboratory facilities could be developed for competition experiments involving large numbers of 50 to 60 mm SL fish, direct tests of competition as a cause for the latter observation could be accomplished. Meanwhile, studies of the physiological ecology of *M. menidia* and *M. beryllina* are necessary in order to determine the metabolic basis of their different life history strategies.

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