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Selective Predation by Larval Striped Bass on Native and Introduced Copepods

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Abstract.—Year-class strength of striped bass *Morone saxatilis* is often determined by the success of first-feeding larvae. In the Sacramento–San Joaquin estuary, this success may be influenced by the recent invasion of exotic copepods that appear to be displacing native copepods important as food. We tested selection by larval striped bass on native copepods (*Eurytemora affinis* and *Cyclops* sp.) and on introduced copepods (*Sinocalanus doerri* and *Pseudodiaptomus forbesi*). Two-species and single-species tests established the following order of preference: *Cyclops* sp. (most preferred), *E. affinis*, *P. forbesi*, and *S. doerri* (rarely eaten). Tests to evaluate the underlying mechanism of prey selection showed that the presence of egg sacs and copepod size did not affect the larvae's choice of prey. Instead, selection by larval striped bass apparently involved differences in copepod swimming and escape behaviors.

Populations of striped bass *Morone saxatilis* have declined markedly in the Sacramento–San Joaquin estuary since 1977 (Stevens et al. 1985). Previous studies have determined that the estuary's striped bass populations are affected by survival rates during the first 60 d of life (Eldridge et al. 1981, 1982) and that survival is correlated with changes in environmental conditions, especially the amount of freshwater inflow, the amount of water being diverted from the upper estuary, and the availability of food organisms (Turner and Chadwick 1972; Stevens 1977; Stevens et al. 1985).

One of the major changes in the food supply of larval striped bass in the Sacramento–San Joaquin estuary in recent years has been the invasion of two oriental copepods, *Sinocalanus doerri* and *Pseudodiaptomus forbesi*, as the result of ballast water releases in 1978 and 1987, respectively (Orsi et al. 1983; Carlton 1985). Both species are now seasonally abundant in the estuary (California Department of Fish and Game, unpublished data). The increase in the numbers of exotic copepods has been associated with the decline in abundance of the native copepod *Eurytemora affinis*, the principal food of larval striped bass, although the decline was already under way by 1972 (Orsi and Mecum 1986).

Meng + Orsi (1991)

The decline of *E. affinis* is presumably a reflection of decreasing phytoplankton abundance and decreasing freshwater inflow (Stevens et al. 1985; Orsi and Mecum 1986), but interactions with introduced copepods may prevent the species' recovery (Orsi et al. 1983). The addition of the t exotic species has slowed the decline in copep numbers in the upper estuary (Orsi et al. 198 California Department of Fish and Game, unpu lished data), but the exotic species may not readily available to striped bass larvae. *Sinocal nus doerri* tends to be found at lower saliniti than *E. affinis* (Orsi et al. 1983), and its long antennae (used to assist swimming) may bett enable it to escape predation by larval fish (Figu 1). *Pseudodiaptomus forbesi* is morphologica similar to *E. affinis*, but it seems to prefer warm water, and it becomes abundant after larval fi numbers have peaked (California Department Fish and Game, unpublished data).

Despite the ecological differences between t two exotic copepods and *E. affinis*, the exotic sp cies cooccur with striped bass larvae frequent enough to be potentially important in larval die and to compensate for the decline in *E. affi* availability. Food availability is an important fa tor in the survival of larval striped bass in est aries (Daniel 1976; Eldridge et al. 1981, 198 Chesney 1989). The purpose of our study was compare the abilities of 7–8-mm striped bass la vae to capture *E. affinis*, *S. doerri*, *P. forbesi*, a a fourth species of copepod, *Cyclops* sp. *Cyclo* sp. is a native to the freshwater portions of t estuary and is occasionally important in the di of larval striped bass (California Department Fish and Game, unpublished data). The null h pothesis tested was that there are no differenc

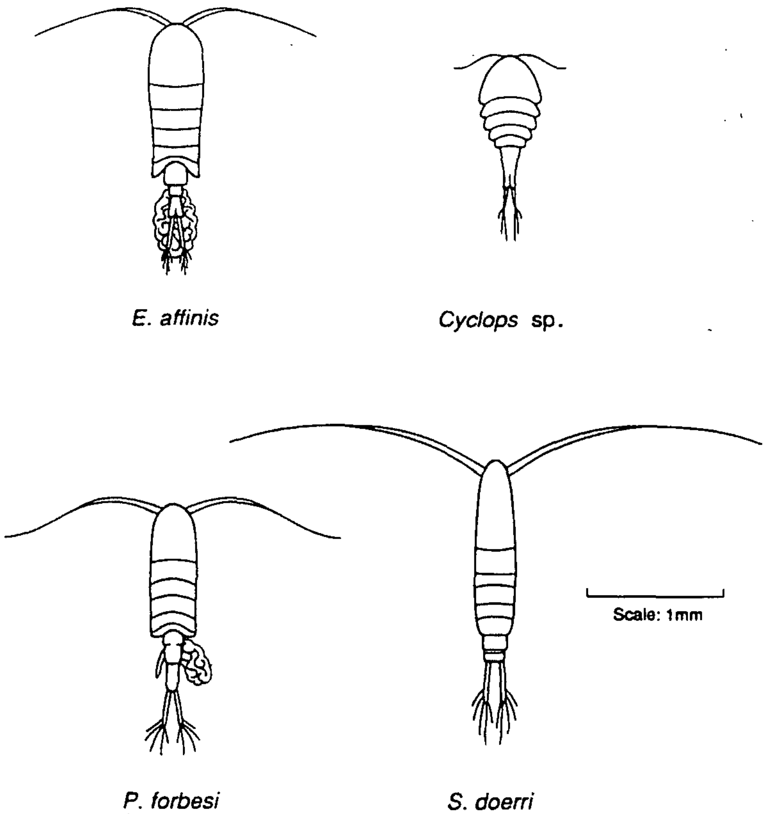

FIGURE 1.—Four species of copepods from the Sacramento–San Joaquin estuary used in feeding trials of p selection by larval striped bass.

in the ability of striped bass larvae to capture the four species of copepods. We also examined aspects of copepod biology that might influence their vulnerability to predation of larval striped bass, including size, behavior, and the presence of egg sacs.

Methods

Striped bass larvae from the California Department of Fish and Game Central Valley Hatchery were transferred to laboratory facilities at the University of California, Davis, 4 d after hatching every week for 10 weeks from April to June 1989. They were raised in 20-L aquaria at 17°C and 3‰ salinity on *Artemia* sp. nauplii until they were about 7 mm long (about 2–3 weeks).

Copepods were collected at various locations throughout the estuary two or three times a week. Drift tows were made for 5–10 min with 80-μm-mesh plankton nets. The copepods were held at 17°C no longer than 3 d before they were used in an experiment. A dissecting microscope (10–30×) equipped with an ocular micrometer was used to sort the copepods by species and sex. Only adu
were used in experiments and care was taken
acclimate them for several hours to any chan
in salinity.

Feeding tests were run in 2-L beakers contain
1 L of water at 17°C and 3‰ salinity. Each bea
held four larvae (7–8 mm) and 60 copepods
of each species in two-species tests). The fish w
acclimated to the beakers and deprived of f
for at least 24 h before the experiment. Beca
there is a difference in size between copepod sex
copepod combinations were assigned to minim
this difference. All experiments were conduc
under constant low light from a combination
fluorescent and incandescent sources. An *Arte*
sp. control was used in each experiment. If
Artemia sp. were eaten in the control beaker,
experiment was not used in the analysis. Fo
four experiments were run, each replicated th
or four times. Each of the four copepod spe
was tested alone and in combination with the o
er species; six combinations plus four single-s
cies tests were possible.

Each feeding trial lasted 2.5 h; this period was dictated by digestion rates. Experiments were ended by pouring the contents of each beaker through a fine net and preserving them in 70% ethanol. Beakers with dead fish were not used in the analysis. The standard length of each fish was measured with the ocular micrometer, and the presence or absence of an inflated swim bladder was noted. Stomachs were removed and numbers and species of copepods eaten were recorded. Periodically, counts of uneaten prey remaining in the beaker were compared with stomach analysis counts to verify the results. From each replicate a random subsample of each copepod species was measured and recorded (Table 1).

We also examined some of the possible mechanisms underlying selection by larvae; in particular, we compared the effects of copepod sizes, behaviors, and presence or absence of egg sacs on larval selection. To analyze the effect of egg sacs, separate tests were done on *E. affinis* and *P. forbesi* females with and without egg sacs. Size selection was evaluated with male and female *E. affinis*. Observations of the experiments and simulated predation with a pipette provided information on copepod behavior.

The two-species tests were analyzed with a chi-square test of independence. Replicates were pooled and total numbers eaten were used to compute the statistic. Sample size for each combination varied from 6 to 18 replicates. Thus, to compare the values of the chi-square statistic as a measure of preference, it was necessary to standardize the sample size. Of the six combinations, four had to be standardized; this was done by random draw. The draws were repeated 10 times and the mean chi-square was used for that combination. Sample sizes of the single-species tests and the experiments on the underlying mechanisms of selection were not standardized. The Kruskal–Wallis rank test (Sokol and Rohlf 1981) was used to determine if there were significant differences among the single-species tests. The experiments that evaluated the underlying mechanisms of prey selection were analyzed with chi-square. Analysis of variance was used to determine significant differences in size between species and between male and female *E. affinis*.

Results

Two-Species Tests

In four of the six combinations of two species, there were significant differences (df = 1, $P < 0.01$) in the selection of copepod prey by larval fish (Table 2). In every test that included *S. doerri*, it was negatively selected. *Pseudodiaptomus forbesi* was negatively selected when combined with *Cyclops* sp., but it was preferred to *S. doerri*. When *P. forbesi* was combined with *E. affinis*, there were no significant differences in prey selection. Offering the fish a combination of the two native species, *E. affinis* and *Cyclops* sp., also produced no significant differences.

TABLE 1.—Numbers and mean sizes of copepods offered to striped bass larvae.

Prey	*N*	Mean size ± SD (mm)
Cyclops sp.	93	1.3 ± 0.2
Eurytemora affinis	97	1.4 ± 0.1
Females	20	1.46 ± 0.07
Males	20	1.23 ± 0.09
Pseudodiaptomus forbesi	99	1.3 ± 0.1
Sinocalanus doerri	92	1.5 ± 0.1

A comparison of chi-square as a measure of prey selectivity showed that preference between species increased markedly when *S. doerri* was included in the combination. When *S. doerri* was offered with *P. forbesi*, *Cyclops* sp. and *E. affinis*, the chi-square values were 11.0, 15.0, and 15.7, respectively, compared with 2.2, 1.5, and 6.7 in the absence of *S. doerri*. The other significant combination was *Cyclops* sp. versus *P. forbesi* ($\chi^2 = 6.7$). Trends in prey selection did not change after the sample sizes were adjusted for four of the combinations (Table 2).

When *Cyclops* sp. was offered in two-species tests, it was always preferred. *Eurytemora affinis* was the next-most selected copepod, followed closely by *P. forbesi*; *S. doerri* was rarely eaten.

Single-Species Tests

The results of the single-species tests supported the results of the two-species tests. The Kruskal–Wallis rank test showed significant differences between the numbers eaten in each single-species test ($H = 18.6$, df = 3, $P < 0.001$). When this statistic was calculated without *S. doerri*, it was still significant ($H = 6.4$, df = 2, $P < 0.05$). Mean numbers eaten per trial were 18.3, 12.5, and 9.6 for *Cyclops* sp., *E. affinis*, and *P. forbesi*, respectively (Table 3). No *S. doerri* were eaten.

Possible Mechanisms of Prey Selection

The results of the experiments conducted to understand mechanisms underlying larval selection of copepods were not significant (Table 4). In sep-

TABLE 2.—Total numbers of copepods eaten in two-species tests. Chi-square error for adjusted sample size is ± 1 SD. Sample size was adjusted by random draw. Asterisks denote $P < 0.01$, df = 1.

	Unadjusted sample size			Adjusted sample size	
Combination of prey	Number of replicates	Number eaten	χ^2	Number of replicates	χ^2 ± SD
Eurytemora affinis/*Pseudodiaptomus forbesi*	18	203/162	2.2	6	0.63 ± 0.66
Cyclops sp./*Eurytemora affinis*	6	22/11	1.5		
Cyclops sp./*Pseudodiaptomus forbesi*	6	70/32	6.7*		
Pseudodiaptomus forbesi/*Sinocalanus doerri*	7	32/2	12.4*	6	11.0 ± 1.3*
Cyclops sp./*Sinocalanus doerri*	7	37/0	17.5*	6	15.0 ± 2.1*
Eurytemora affinis/*Sinocalanus doerri*	8	45/0	21.5*	6	15.7 ± 1.8*

arate tests of predation on *E. affinis* and *P. forbesi* with and without egg sacs, there were no significant differences in numbers eaten ($\chi^2 = 0.10$ and 0.94, respectively; df = 1). Although there were differences in size between species ($F = 24.6$, df = 3, 36, $P < 0.001$) and between male and female *E. affinis* ($F = 75.9$, df = 1, 42, $P < 0.001$), there was no difference ($\chi^2 = 0.16$, df = 1) in selection between the two sizes.

Observations during the experiments and during simulated predation with a pipette indicated that copepod swimming and escape behavior differed. The main difference among the four copepods was length of time spent in fast or slow motion. *Eurytemora affinis* and *P. forbesi* spent most of their time gliding slowly in straight lines. The gliding was broken by sudden darts of less than a centimeter to change directions or when threatened by a predator. *Cyclops* sp. swam in erratic spiraling patterns broken by sinking, and it lacked a noticeable escape response. *Sinocalanus doerri* hung in the water with its exceptionally long antennae fully extended at right angles to its body. This hanging behavior was broken by series of rapid jumps of up to 3 cm in unpredictable directions, even when the copepod was not threatened. The long antennae snapped back with each burst.

There was also a difference in behavior between fish with and without inflated swim bladders. Those with inflated swim bladders had a 50% chance of capturing a copepod, whereas fish with uninflated swim bladders had only a 25% chance of feeding success.

TABLE 3.—Total numbers of copepods eaten by striped bass larvae and average number per trial in one-species tests. Sixty copepods were available for each trial.

		Numbers of copepods eaten	
Prey species	Number of trials	Total	Mean ± SD
Cyclops sp.	3	55	18.3 ± 5.8
Eurytemora affinis	4	50	12.5 ± 0.6
Pseudodiaptomus forbesi	8	77	9.6 ± 4.7
Sinocalanus doerri	8	0	

Discussion

Two-Species and Single-Species Tests

Larval striped bass showed clear preferences among copepod prey. The native copepods were preferred to the introduced species in this order: *Cyclops* sp. (most preferred), *E. affinis*, *P. forbesi*, and *S. doerri* (only two eaten in 44 experiments). When offered a choice of the two native copepods, the fish showed no clear preference. However, *Cyclops* sp. is a freshwater species and is only available to the larvae early in the season or during years of exceptionally high outflow, so *E. affinis* is more important as a food item. The larval fish also did not discriminate strongly between *E. affinis* and *P. forbesi*, indicating that *P. forbesi* may be a suitable food for young striped bass. However, *P. forbesi* does not become abundant until late spring. In 1988, *P. forbesi* was first seen in stomachs of larvae in the last week in June (Lee Miller, California Department of Fish and Game,

TABLE 4.—Experiments on prey attributes that may affect prey selection by larval striped bass. All copepods used in the egg sacs–no egg sacs experiments were females. Differences in prey selection due to size were compared with male (1.2 mm) and female (1.5 mm) *E. affinis*.

Prey and attribute	Number of replicates	Number eaten	χ^2
Eurytemora affinis			
Egg sacs/no egg sacs	10	60/66	0.10
Pseudodiaptomus forbesi			
Egg sacs/no egg sacs	4	38/52	0.94
Eurytemora affinis			
Males/females	5	28/23	0.16

adjusted sample size is ± l

Adjusted sample size	
Number of repli-cates	χ^2 ± SD
6	0.63 ± 0.66
6	11.0 ± 1.3*
6	15.0 ± 2.1*
6	15.7 ± 1.8*

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Num-ber of repli-cates	Number eaten	χ^2
10	60/66	0.10
4	38/52	0.94
5	28/23	0.16

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personal communication). Thus, unless its distribution expands temporally, *P. forbesi* will never be an important food for larval striped bass.

Because *Cyclops* sp. and *P. forbesi* usually do not cooccur with first-feeding striped bass, *E. affinis* emerges as the most important food for the larvae, and this agrees with the most recent food-habits data available from the California Department of Fish and Game (Table 5). The abundance of *E. affinis* peaks at the height of the striped bass spawning season. *Sinocalanus doerri* is also abundant at this time, but it is not eaten until the fish reach 9–10 mm (California Department of Fish and Game, unpublished data). When the fish reach this length, the critical first-feeding stage is over. Thus, it appears that the success of the first-feeding larvae and the resulting strength of the year-class depend on the cooccurrence of larval striped bass with *E. affinis*. Analogous critical pairings between certain copepod species and larval fishes occur in the ocean (Cushing 1975).

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Mechanisms Underlying Prey Selection

Although the introduction and spread of *S. doerri* compensated for declines in the copepod component of the zooplankton (due to declines of *E. affinis*), *S. doerri* has not taken the place of *E. affinis* as larval striped bass food. One of the most obvious differences between *E. affinis* and *S. doerri* is the fact that *E. affinis* carries egg sacs whereas *S. doerri* does not (Figure 1). The sacs may hamper the escape response of *E. affinis* or make the copepod more visible, but our tests did not reveal any significant difference in selection of *E. affinis* with or without egg sacs.

TABLE 5.—Food-habit data collected in 1986 from stomachs of 7-mm larval striped bass (N = 754) in the Sacramento–San Joaquin estuary by the California Department of Fish and Game, Bay–Delta Project, Stockton. *Pseudodiaptomus forbesi* ~~was not~~ introduced until 1987, so ~~does not~~ appear in this study because data on striped bass food since 1987 are not yet available.

Food item	Estimated mean dry weight (μg) of predominant zooplankton in larval striped bass stomachs
Eurytemora affinis	4.03
Cyclops sp.	1.96
Sinocalanus doerri	0.49
Copepodids	0.84
Nauplii	<0.01
Other copepods	0.85
Other zooplankton (includes cladocerans, malacostracans, and rotifers)	1.68
Total	9.86

Although there are significant differences between the sizes of the different copepod species and sexes, we could not find any differences in prey selection when we compared male and female *E. affinis*. The size difference between the sexes is approximately 0.25 mm and is greater than the mean differences between any of the species (0.1–0.2 mm).

Apparently, the gliding motion broken by short darts makes *E. affinis* and *P. forbesi* more vulnerable to predation than the jumping behavior makes *S. doerri*. The erratic swimming of *Cyclops* sp. appears to be difficult to track, but the relatively small volume of water traversed during this spiraling activity may make this species easier to attack. Another important factor is the amount of time each species spends in motion, which increases prey visibility and reactive distance (O'Brien 1979). Thus, the fairly constant movement of *Cyclops* sp. makes it more vulnerable to predation, whereas the hanging behavior of *S. doerri* may make it more difficult to detect.

Escape behavior probably also involves the visibility of these copepods. *Cyclops* sp. is stout and often deeply pigmented, whereas *S. doerri* is slender and whitish, almost translucent. *Eurytemora affinis* and *P. forbesi* are intermediate in body shape and coloration. Understanding the relationship between visibility and escape behavior will require more rigorous investigation.

Predator–prey interaction is also affected by the inflation of the swim bladder. Fish with uninflated swim bladders must wiggle and swim constantly to avoid sinking, whereas fish with inflated swim bladders are able to hang motionlessly. An inflated swim bladder reduces energy expenditure and gives larval fish the advantage of neutral buoyancy for capture success. Only 25% of the fish with uninflated swim bladders experienced feeding success.

We conclude that the mechanism underlying prey selection by larval striped bass is behavioral and we propose that learning and swimming behaviors of larval fish interact with differences in copepod swimming and escape behavior to determine first-feeding success for the larvae. Introduced species and environmental disturbances have changed the planktonic foods of the estuary. Although declines in prey density have been partly offset by introduced species, inherent differences among prey types may affect the survival and growth of larval striped bass.

Acknowledgments

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