AGE-SPECIFIC VULNERABILITY OF PACIFIC SARDINE, *SARDINOPS SAGAX*, LARVAE TO PREDATION BY NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

To a large degree interannual variability in recruitment determines the size of pelagic fish populations. Recruitment to the Pacific sardine, *Sardinops sagax*, population off California varies from year to year over several orders of magnitude and is unrelated to spawning stock size (Murphy 1966; MacCall 1979). Variable mortality rates in the first year of life must determine year-class strength, although the sources of this variability are unknown. Mortality rates in the earliest stages are size specific with highest rates in the egg and yolk-sac stage (Ahlstrom 1954; Butler 1987) and may contribute to variability in year-class strength (Smith 1985).

The sources of mortality of sardine larvae have yet to be investigated. In other pelagic larvae, mortality is due to either starvation or predation, and starvation is significant only during the brief period after the onset of feeding (O'Connell 1980; Hewitt et al. 1985; Theilacker 1986; Owen et al. 1987). In sardines, significant mortality occurs during the egg and yolk-sac stages (Ahlstrom 1954) and this mortality can only be due to predation. Variable mortality in older larval and juvenile sardines may also contribute to variability in recruitment, and this mortality, as in other fishes, may also be due to predation (Hunter 1984).

The objective of this paper was to determine the size-specific vulnerability of Pacfiic sardine larvae to predation by adult northern anchovies, *Engraulis mordax*. The vulnerability of cape anchovy and northern anchovy larvae to

cannibalism has been investigated by Brownell (1985) and Folkvord and Hunter (1986) and found to be an important source of mortality. In this paper the vulnerability of sardine larvae will be compared with that of anchovy larvae and differences in the biology of sardines and anchovies will be discussed.

Our approach was to observe the avoidance behavior of Pacific sardine larvae in response to predatory attacks by northern anchovy adults. Adult northern anchovy were chosen as a predator because the northern anchovy was the most abundant pelagic fish in the California Current region during the waning years of the sardine fishery and because its planktivorous diet includes fish eggs and larvae (Loukashkin 1970; Hunter and Kimbrell 1980).

Materials and Methods

Experimental Fishes

The Pacific sardine larvae used in the experiments were reared from eggs spawned in the laboratory. Adult Pacific sardines were collected off San Diego and held in 175 m^3 aquarium for six months. Males and females with developing gonads were isolated in spawning tanks and injected with 250 mg human chorionic gonadotropin and on the following day injected with 200 units pregnant mare serum and 20 mg salmon pituitary extract. On the third day fertilized eggs were collected from the spawning tank. Larval rearing procedures follow those described by Hunter (1976). Temperature in the rearing tanks was maintained at 21°C.

Apparatus and Procedures

Experimental apparatus and procedures were the same as those described by Folkvord and Hunter (1986) but will be briefly outlined here. Experimental predators were two groups of 5 adult northern anchovy (range of standard lengths 8.4–9.2 cm). Predators were maintained in two rectangular fiberglass tanks (0.75 × 2.15 × 0.83 m = 1.35 m^3) and fed adult brine shrimp except on days of experimental observation. Seawater was supplied continuously to the tanks except during experiments. The temperature in the observation tank ranged from 16.2° to 22.8°C (mean = 20.1°C). Two 100 W incandescent lamps produced 2,000–3,000 mc at the surface of each tank. A black plastic tent enclosing a window on

one side of the tank provided a darkened observation chamber.

Each trial consisted of the encounter of three prey with the predators. Prey were introduced into the observation tank with a clear glass beaker. Initial feeding behavior of the predators is quite variable but becomes less variable as the predators become accustomed to prey in the tank. For this reason, prior to each experiment adult *Artemia* were introduced as prey for five consecutive trials to standardize predator behavior. After the preliminary trials with *Artemia*, three trials with sardine larvae were alternated with one trial with brine shrimp until 18 trials with sardine larvae were completed. Each experiment was concluded with a trial of brine shrimp to test for satiation.

The number of observations for each larval size class was the total number of predator-prey interactions observed among larvae in that size class. The mean standard length was determined from 20 larvae sampled randomly from the rearing tank on the day of each behavior experiment. The numbers of observations for each size class (mean SL) were 8.0 mm, 41; 11.3 mm, 51; 12.1 mm, 114; 12.7 mm, 46; 14.1 mm, 81; 17.6 mm, 104; and 19.6 mm, 69. Experiments were not extended to larger sizes due to insufficient numbers of larvae.

Classification of Behavior

Prey behavior was scored only when the predator attacked a prey. Four measures of predator-prey interactions were calculated: predator attack distance, the distance from which the predator responded to the prey and initiated its attack; frequency of avoidance response; frequency of escapes; and predation rate (percentage of larvae captured during the 5-min trials). An avoidance response was a change in speed or trajectory of a larvae before the predator had completed its attack by closing its mouth. An escape was defined as a larval response in which the predator failed to capture the larvae in a single attack. Typically adult anchovy make a single attack on a prey item and do not pursue a prey that escapes (Folkvord and Hunter 1986) but rather continue searching the tank. Thus attacks on one prey item were recorded twice if the first attack was unsuccessful. Although predator attack distance was recorded, this measurement is highly subjective and comparison with the measurements of other observers is suspect. We did not analyze predator attack distance for this reason.

To compare response and escape behaviors of Pacific sardine with those reported by Folkvord and Hunter (1986) for northern anchovy at similar stages of development, mean lengths were converted to ages using field growth rates back-calculated from otolith increment widths for each species. Confidence limits of the percentage of larvae responding or escaping attack were estimated assuming the binomial distribution.

Results

Probability of Response to Attack

The youngest larval stages of both sardine and anchovy were the most vulnerable to predation. Only 17% of 8 mm sardine larvae (smallest size tested) responded to attack by adult anchovy. With increasing size more sardine larvae responded to attack. At 20 mm, the largest size tested, 61% of the larvae responded to attack. The response rate of Pacific sardine larvae was consistently lower than that of northern anchovy larvae of similar lengths (Fig. 1). Although this difference in responsiveness could be due to differences in the observer, it may also be explained by the difference in age of anchovy and sardine at the same length. Sardine larvae are about 6.2 mm when they begin feeding (age = 5 days from fertilization at 17°C), whereas first-feeding anchovy larvae are only about 4.3 mm (age = 5 days from fertilization at 17°C) (Zweifel and Lasker 1976). Sardine larvae also grow faster than anchovy lar-
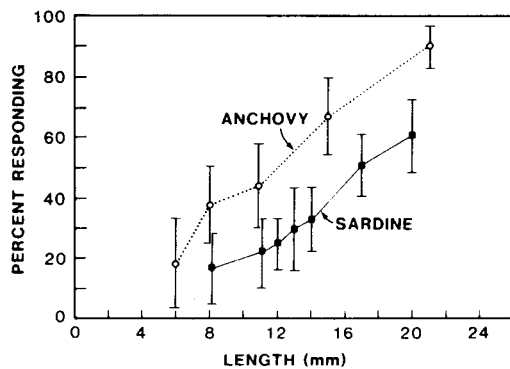
vae at the same temperature (Butler and Rojas de Mendiola 1985). Thus, sardine larvae are younger at a given size than anchovy larvae.

Since the latency of response to attack must be related to the development of the central nervous system (Webb 1981; Webb and Corolla 1981), it may be more appropriate to compare sardine larvae with anchovy larvae of the same age. For that reason lengths of the larvae of both species were converted to age using growth rates measured in the field (Methot and Kramer 1979; Butler 1987). Comparison of the percentage of larvae responding to attack at a given age (Fig. 2) reveals no significant difference in the rate of development of response to attack. Thus, the escape response develops at the same rate in Pacific sardine and northern anchovy, and the difference in proportion of larvae responding at a given size (Fig. 1) is due to the difference of size at hatching and the difference in growth rates of the two species.
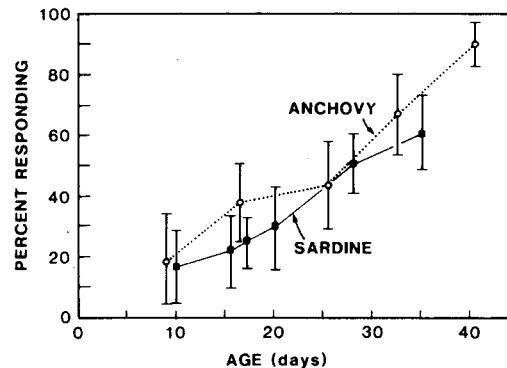
FIGURE 2.—Increase by age of the percentage of Pacific sardine larvae, *Sardinops sagax*, and northern anchovy larvae, *Engraulis mordax*, responding to attack by adult northern anchovy and 95% confidence intervals. Size categories of reared larvae have been converted to ages using growth rates estimated from the field. Data on anchovy larvae from Folkvord and Hunter (1986).

FIGURE 1.—Increase by size of the percentage of Pacific sardine larvae, *Sardinops sagax*, and northern anchovy larvae, *Engraulis mordax*, responding to attack by adult northern anchovy and 95% confidence intervals. Data on anchovy larvae from Folkvord and Hunter (1986).

Probability of Escaping Attack

The ability to successfully avoid attack increased with size of Pacific sardine as well as northern anchovy. Few small larvae of either specie escaped attack by adult northern anchovy. Only 3% of 8 mm sardine larvae escaped attack and the percentage of larvae escaping increased to only 11% for 17 mm larvae and 13% for 20 mm

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larvae (Fig. 3). The proportion of small anchovy larvae escaping attack was also low (6%) but increased with size to 73% of 22 mm larvae (Folkvord and Hunter 1986). The numbers of larvae escaping attack were significantly different between anchovy and sardines at sizes larger than about 13 mm. Conversion of lengths to age using field growth rates does not eliminate the differences between sardine and anchovy (Fig. 4). Sardine larvae older than 20 days were more vulnerable to predation than anchovy larvae of the same age (Fig. 4).

FIGURE 3.—Increase by size of the percentage of Pacific sardine larvae, *Sardinops sagax*, and northern anchovy larvae, *Engraulis mordax*, escaping attack by adult northern anchovy and 95% confidence intervals. Data on anchovy larvae from Folkvord and Hunter (1986).

FIGURE 4.—Increase by age of the percentage of Pacific sardine larvae, *Sardinops sagax*, and northern anchovy larvae, *Engraulis mordax*, escaping attack by adult northern anchovy and 95% confidence intervals. Size categories of reared larvae have been converted to ages using growth rates estimated from the field. Data on anchovy larvae from Folkvord and Hunter (1986).

Discussion

The proportion of Pacific sardine larvae responding to attack and escaping attack increased with size and with age. Our results differ from those reported by Folkvord and Hunter (1986) for anchovy larvae in the rate at which sardine larvae respond and escape attacks at given sizes and ages. It should be noted that, although the methodology was the same, the observers were different. This difference could affect rate of response to attack. It also should be noted that the size of adult anchovy used by Folkvord and Hunter (1986) ranged from 83 to 89 mm SL, whereas the size range was 84–95 mm SL in our study and that the size of predator influences the number of larvae escaping (Folkvord and Hunter 1986). The slightly larger size of predators used in this study is not sufficient to explain difference in escapement, nor is the difference in observer likely to affect the rate of escapement since the observer's task is to examine whether the larvae are escaping or are being eaten.

The greater vulnerability to predation of sardine larvae than anchovy larvae has interesting implications. In general, larger larvae are less vulnerable to predation than small larvae. Bailey (1984) and Bailey and Batty (1983) compared the vulnerability of cod, flounder, plaice, and herring larvae to predation by invertebrate predators. They found that herring larvae were the least vulnerable larvae because herring were more reactive and had the greatest escape speeds. Sardine larvae are larger at hatching and at a given age are larger than anchovy larvae. In our experiment sardine larvae react to predatory attacks at similar rates as anchovy larvae, but escape attack at a much lower rate.

This difference in vulnerability to attack may be due to differences in swimming behavior. Anchovy larvae swim using beat and glide locomotion (Hunter 1972). The escape behavior is usually a burst of swimming from a motionless position (Folkvord and Hunter 1986). We observed that sardine larvae, however, swim continuously and they respond to attack by changing direction and increasing speed. This difference in swimming mode may affect escape behavior in two ways. The escape behavior of sardine larvae may be less flexible than that of anchovy larvae because the direction the sardine larvae takes is largely determined by its trajectory. Since sardine larvae cruise, their scope for activity (escape behavior) may be limited. Anchovy larvae accel-
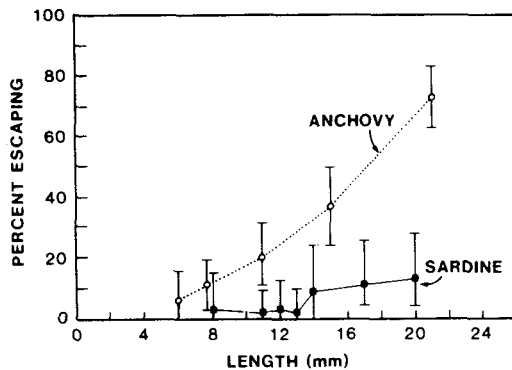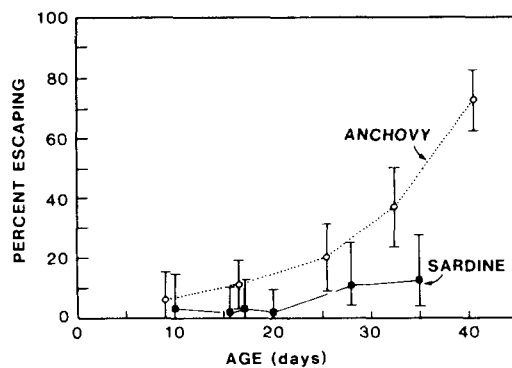
erate from a standing start and have the possibility of moving in a number of directions. We speculate that the beat and glide behavior of anchovy larvae may not only be hydrodynamically more efficient (Weihs 1974) but also may reduce the vulnerability to predation.

Acknowledgments

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