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PREDATION ON THE PACIFIC SAND LANCE, *AMMODYTES HEXAPTERUS* (PISCES: AMMODYTIDAE), DURING THE TRANSITION BETWEEN DAY AND NIGHT IN SOUTHEASTERN ALASKA.—

The Pacific sand lance, *Ammodytes hexapterus*, is particularly vulnerable to predators during a changeover between distinctive diurnal and nocturnal modes of behavior. This conclusion developed from observations in southeastern Alaska during 10 days of May 1978. At that time, sand lance (110-150 mm SL) were attacked by a variety of predators in a small cove (area about 2 ha, maximum depth about 25 m) at the head of Steamer Bay, Etolin Island (56°N, 133°W). Twelve hours of general observations spread over the diel cycle showed predation on

sand lance concentrated during the transition between day and night. Between 1800, when diurnal conditions still prevailed and 0030, when nocturnal conditions had been in force for some time, I spent 5 hr over five evenings observing interactions between sand lance and specific predators. (No observations were made during the morning changeover between night and day.)

Intensified evening predation occurred while most of the sand lance were moving from an active mode in the water column to a resting mode in the sediments. This changeover was part of a diel pattern of movements between a feeding ground, nearby schooling sites and a refuge in the sand. The feeding ground was at the cove's entrance, where the sand lance foraged when tidal currents flowed into the cove during the day. At these times the sand lance joined Pacific herring, *Clupea harengus pallasii*, in mixed aggregations and fed vigorously on zooplankton throughout the upper levels of a 10 m water column. (A planktivorous diet appears to be characteristic of *Ammodytes* spp., Macer, 1966; Reay, 1970; Scott, 1973.) At other times of the day most of the sand lance were in dense, monospecific schools that moved slowly several meters above the bottom, within about 100 m of the cove's entrance. Feeding by members of these schools was much reduced and limited to individuals at the schools' edges. Often the schools were near one particular patch of coarse sand, about 0.1 ha in area, that sloped sharply between depths of about 5 and 10 m near shore, approximately 75 m from the cove's entrance. Except at this one spot the cove was floored by silt, fine sand, gravel, cobble and larger rocks. The patch of coarse sand was the sand lance's refuge, probably because it was a relatively loose, porous substrate conducive to burrowing. Reportedly similar sediments are refuges for *A. americanus*, an Atlantic Ocean species (Meyer et al., 1979).

Using the numbers of sand lance flushed when the substrate was disturbed as an index to the numbers buried, it was determined there were at least some in the sediments of the refuge at all times during the diel cycle. (Often sand lance were flushed when I simply swam close to the bottom.) Relatively few were there by day, however, while at night these sediments seemed to contain virtually all the sand lance in the cove. Widespread inspection of sediments elsewhere in the cove after dark flushed only an occasional individual and extensive search of the nocturnal

water column found none. Describing a similar situation in the Baltic Sea, Kühlmann and Karst (1967) reported that almost all the sand lance in their study area foraged offshore during the day and burrowed in one particular nearshore sand bank at night.

It was difficult to determine when the evening changeover began. Sunset was at about 2200 (Pacific Daylight Savings Time; Nautical Almanac, US Naval Observatory), but could not be observed on the evenings involved here owing to either clouds at the study site or my being underwater at the time. Nevertheless, daylight was greatly diminished underwater by 2030, when the sand lance moved in several small schools over central parts of the refuge where I had not seen them earlier in the day. Periodically, these schools descended to within a meter of the substrate, at which point individuals and small groups dove from the schools into the sand.

At about the same time, predators began to concentrate in the refuge and to station themselves under the slowly moving schools. Four species of predators were consistently present: rock sole (*Lepidopsetta bilineata*), starry flounder (*Platichthys stellatus*), great sculpin (*Myoxocephalus polyacanthocephalus*) and whitespotted greenling (*Hexagrammos stelleri*). All four are sedentary forms that attack from positions at rest on the substrate. Although numerous in the refuge when sand lance were entering the sediment in large numbers, the predators were not concentrated there during observations made at other times.

As the sand lance schools moved slowly over the refuge, the predators followed along beneath them and intensified their attacks. The predators, however, did not strike at individuals that were in the schools or in the act of diving into the sand. Rather, they struck at individuals that had entered the sand, but which appeared to be having difficulty settling into a resting spot. The sole and flounder seemed responsive to movements of the sand above restless sand lance and attacked by driving their jaws into the sand, whereas the sculpin and greenling went after sand lance that reappeared after having been buried. These prey of sculpin and greenling may have found their initial resting spots unsatisfactory, because they soon emerged and swam off to settle again elsewhere, or to rejoin the schools. Often these emerging sand lance paused with head protruding from the sedi-

ment—perhaps to look for threatening predators. Then, with a vigorous move, they cleared the bottom and darted away. The sculpin and greenling struck the moment the sand lance emerged from the sand, suggesting their attacks may be even more intensive during the morning changeover, when presumably most of the sand lance emerge from the sand.

One sole (328 mm SL) was speared after it had been seen striking four times at buried prey in the refuge. Its gut contents included four sand lance (about 110 mm SL), but only two of these were fresh enough to have been recently captured. The other two were extensively but similarly digested, indicating they had been captured during some earlier feeding period (perhaps early that morning). The rest of the gut contents, which were in varying stages of digestion and so probably represented feeding throughout the day, consisted of six polychaetes (30–110 mm long) and four limpets (5–10 mm). One sculpin (150 mm SL), speared after attacking an emerging sand lance, contained two of them—one (115 mm) apparently recently captured and the other (about 100 mm SL) extensively digested.

Although certain sand lance seemed vulnerable during initial adjustments to the resting mode, once settled in they appeared secure. This became evident when the predators continued to limit their attacks to sand lance that had just entered the sand, even after buried sand lance became numerous throughout the area. Buried sand lance in the Baltic Sea were similarly judged by Kühlmann and Karst (1967) to be secure from predators throughout the night.

Predation continued unchanged through the developing twilight, except that the sand lance schools became progressively smaller. Although individuals at the edges of the schools sporadically snapped at zooplankton, feeding seemed relatively insignificant during the changeover. I observed small schools of sand lance above the refuge as late as 2230, but on that occasion an exhausted air supply forced me to leave the site. When I returned 30 min later, sand lance no longer occupied the water column and most of the predators were gone. This situation was still in effect when I left the site at 0030.

Despite the limited scope and duration of these observations, probably they have widespread relevance. For example, the diel activity pattern in *A. hexapterus* had many elements in common

with the diel pattern of sand lance in the Baltic Sea (as described by Kühlmann and Karst, 1967). Probably at least most species of sand lance change from an active to an inactive mode during the transition between day and night. Although nocturnally active sand lance have been reported (Senta, 1965), Winslade (1974:574) suggested these may have been individuals drawn from the sea floor by "bright lights of the observing ship." Sand lance are known to be attracted to light at night (Borisov, 1955, cited in Winslade, 1974), but presumably sand lance drawn to lights at the water's surface from resting places on the bottom were not completely buried in the sediment. Probably some keep at least one eye uncovered, which would account for the numbers flushed from the sand when I swam close to, but did not come in contact with, the bottom. Describing the nocturnal behavior of *A. marinus* (an Atlantic Ocean species) in aquaria, Winslade (1974) noted that although most individuals were completely buried in the sand, a few were partially uncovered.

Vulnerability to predators during a changeover between distinctive diurnal and nocturnal modes of behavior is widespread among fishes, but most evidence comes from the tropics (Hobson, 1968; Munz and McFarland, 1973; Major, 1977). If there is a comparable period of crepuscular vulnerability at higher latitudes one would expect it to be extended by the longer twilight there. According to Helfman (1981), the poleward increase in length of twilight explains why temperate lake fishes spend more time than do tropical reef fishes shifting between their diurnal and nocturnal modes. That changeover times increase with latitude was evident in Steamer Bay, where the 2 hr *A. hexapterus* spent in transition more than doubled the changeover period involving all the fishes—both diurnal and nocturnal—on coral reefs in tropical Hawaii (as described by Hobson, 1972). This difference can be related to the lengths of twilight at the two locations. On the dates of the observations involved, Civil Twilight lasted 57 min in Steamer Bay, compared to a mean of about 23 min in Hawaii (Nautical Almanac, US Naval Observatory). And as might have been predicted from this difference, *A. hexapterus* in Steamer Bay experienced intense crepuscular predation over a period that more than doubled the reported duration of intense crepuscular predation on fishes in tropical seas (Hobson, 1968; Major, 1977).

Probably it is at least partly a latitudinal difference that more than 2/3 of the changeover and related predation experienced by *A. hexapterus* occurred before sunset, whereas most of the changeover events among fishes on tropical coral reefs occur after sunset (Hobson, 1972; McFarland et al., 1979). This difference should have been expected if, as most reports have suggested (Collette and Talbot, 1973; Domm and Domm, 1973), the changeover events are a response to specific levels of decreasing daylight, rather than to time of sunset. Daylight faded much earlier relative to sunset in Steamer Bay than it does on tropical coral reefs, not only because the water was less transparent, but also because the sun was low in the sky—virtually on the horizon—for a much longer period immediately before sunset.

The surge in predation among fishes during the transition between day and night is to some extent a consequence of successful adaptations to the two major segments of the diel cycle. Because day and night are so different, appropriate adaptations to each have resulted in widely divergent modes that must be bridged during twilight. Thus, over the diel cycle, *Ammodytes* spp. effectively reduce predation two very different ways—by day they school (Pitcher and Wyche, 1983) and by night they burrow (Kühlmann and Karst, 1967). And as the crepuscular attacks on *A. hexapterus* in Steamer Bay have demonstrated, the transition between these two modes can be perilous.

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- EDMUND S. HOBSON, *Southwest Fisheries Center Tiburon Laboratory, National Marine Fisheries Service, 3150 Paradise Drive, Tiburon, California 94920. Accepted 13 May 1985.*