

PREDATOR-PREY INTERACTIONS IN SCHOOLING FISHES DURING PERIODS OF TWILIGHT: A STUDY OF THE SILVERSIDE *PRANESUS INSULARUM* IN HAWAII¹

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ABSTRACT

Observations of free living and captive silversides were made in Kaneohe Bay, Hawaii, in October and November 1972 and September 1973. The silversides demonstrated changes in schooling behavior associated with changes in light levels during the periods of twilight. During morning twilight, individual silversides formed schools, which in some areas moved from deep water to shallow water over reefs. All silversides remained in large inactive schools in shallow water or along the edge of channels throughout the day. During evening twilight, schools left the reef and/or broke up, with individual silversides spreading out to feed near the surface. Predation upon the silversides, as evidenced by their jumping behavior, was most intense during the twilight periods as schools formed and broke up. Captive silversides, when not in the presence of predators, tended to increase their interfish distance when in diurnal schools. The formation and breakup of schools of these silversides appear to be very similar to behavioral patterns of related and unrelated species of fish in many parts of the world. The formation and break up of silverside schools appear to be related to the threat of predation, the availability of the silverside's food, and the visual sensitivity and thresholds of both the silversides and their predators.

Daily twilight or crepuscular periods are critical ones with respect to predator-prey interactions between many species of fishes, at least in tropical regions of the world. Hobson (1968, 1972), Collette and Talbot (1972), and Domm and Domm (1973) demonstrated the importance of twilight periods on behavioral changes in reef fishes. Hobson (1968, 1972, 1974) suggested that such transitions in behavior are shaped by the threat of predation.

Predation pressure is also clearly a factor in the evolution of schooling behavior in prey species (Breder 1959, 1967; Hobson 1968; Shaw 1970; Radakov 1973). Most reef fishes hide from their predators amongst the interstices of the coral reef. Many surface and open water prey species lack such hiding places and appear to form schools as a means of cover seeking (Williams 1964, 1966), the school serving as a mobile biological refugium especially during daylight hours. During evening twilight periods many such schools break up with individuals spreading out to feed. During morning

twilight periods individuals once again form schools (Hobson 1968, 1972, 1973; Hobson and Chess 1973).

Vision has been shown to be important in the maintenance of schools (Woodhead 1966; Hunter 1968; Shaw 1970; Radakov 1973). In addition, Munz and McFarland (1973) indicated that the behavioral changes of tropical marine fishes during periods of twilight are due to shifts in the visual sensitivity of these fishes with changes in light levels.

The objectives of this study were to determine if schools of the Hawaiian silverside, the iao, *Pranesus insularum*, broke up and reformed in response to light levels occurring during twilight, and to determine how the activity of predators of this species of silverside was related to this behavior.

Study Sites

Field observations were made at two locations within Kaneohe Bay, along the island of Oahu in the Hawaiian chain. These sites were a 10,000 m² area of flat reef (water depth \leq 2 m at high tide) immediately adjacent to the east side of Lilipuna Pier (Dock), and a 2,500 m² area near the central portion of a dredged out (to a depth of 2-3 m)

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"lagoon" adjacent to the Hawaii Institute of Marine Biology (HIMB) on Coconut Island. The northern edge of the reef adjacent to Lilipuna Pier drops abruptly into a 3- to 10-m deep channel, while the southern side is adjacent to the shore.

The reef and channel area near Lilipuna Pier are open to the effects of wind and waves within Kaneohe Bay throughout the year. Occasionally, the winds abate or shift and the bay's surface becomes calm and glassy. The observations reported here could only be made at such times when the estimated wind velocity was less than 2.6 m/s (5 knots). At night near the end of the pier a fixed low intensity incandescent light bulb casts an arc of light out over a small area in the channel. Observations were not made within the area encompassing this arc of light. The waters in the HIMB lagoon are usually calm or only slightly rippled, being protected by a vegetation covered coral rubble peninsula on its normally windward side and thicker, higher, vegetation on its island or leeward side.

Kaneohe Bay is rimmed at approximately 1.6 km inland by mountains that rise to 762-960 m. Throughout each day, dense clouds usually form along these mountains, occluding the sun during the late afternoon. This often results in twilight conditions occurring earlier than would normally be predicted for the bay's position of latitude and longitude.

METHODS

The prey species of fish observed in this study was *P. insularum*, approximately 20-60 mm SL and approximately 0.03-2.45 g wet weight. Observations of the silverside's behavior were made during calm periods in October (7 days) and November (3 days) 1972 and September (5 days) 1973. All observations were made visually from a height of 0-3 m above the surface of the water. The morning observations commenced approximately 115 min prior to the time of sunrise. The evening observation period terminated about 60 min after the time of sunset.

The only attribute monitored quantitatively during the course of the observations was the jumping escape behavior of the silversides in response to attacking predatory fishes. Enumerating the jumps became a shorthand method of quantifying the number of predatory attacks in the calm areas studied because jumping was

observed to be the primary means of escaping predators once an attack occurred. *Pranesus insularum* was the only prey species observed to jump in the above areas during the periods of this study. The success of predators at capturing prey during the attacks was not determined. Hobson (1968) used a similar method to quantify the number of times leaping predatory cabrilla, *Mycteroperca rosacea*, attacked flatiron herring, *Harengula thrissina*, in the Gulf of California.

During periods of darkness or reduced light, when visual observations under existing light were not possible, jumping by schools of prey could be heard within the areas studied by careful listening; this could only be done when there was no wind and the surface of the water was calm. The time at which schools broke up or reformed during twilight was estimated by listening to changes in the sound of jumps made by multiple and single prey close by, or with a flashlight beam which was quickly turned on and off in one spot, or swept rapidly across the surface of the water from above, and/or held underwater within 0.3 m of the surface. Whether the silversides were schooling or spread out could be readily determined when the fish were illuminated by the beam of light.

Light measurements were made above the surface of the water with a photometer (Weston Ranger 9 universal exposure meter).³ Readings taken with this photometer were compared with those made with a Gossen foot-candle meter and a Spectra-Combi 5000 Model photometer (Photo Research, Burbank, Calif.). The readings obtained during twilight periods were comparable to those given by Brown (1952).

The observations and events reported here are related to the time of sunrise, sunset, and the periods of morning and evening civil and nautical twilight. The two periods of twilight are defined by the angular distance of the sun below the horizon, 0° to -6° for civil twilight, and -6° to -12° for nautical twilight. Fish respond directly to the amount and type of light present, which is influenced by astronomical as well as local environmental conditions. However, the use of these terms and that of the corresponding angular distance of the sun below the horizon is of immense value when comparing the observations of many investigators working in different loca-

³Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

tions at different times of the year and under different environmental conditions.

BEHAVIOR OF FREE-LIVING SILVERSIDES

Between sunrise and sunset each day hundreds to thousands of individual silversides could be observed in large, often elongated, schools along Lilipuna Pier and other structures over shallow reefs, along the edge of reefs, and in quiet protected waters such as the HIMB Lagoon. At times the silversides remained in the shadow of structures or overhanging vegetation, rarely venturing into sunlit water. The schools were located just under the surface of the water, with individuals often forming single or multitiered layers. The schools as a whole were largely stationary and inactive except for the occasional individual that darted out from and immediately returned to a school. These individuals appeared to be feeding, snapping at objects which I could not see when they left the school. While in the large inactive schools, individuals about one-half to two body lengths apart were randomly oriented to one another. However, upon the approach of a predator or potential predator, or when attacked, the individuals rapidly became polarized, often less than a body length apart as the school maneuvered about the predator(s) in well coordinated patterns.

When a predator slowly approached a school of silversides it frequently penetrated into the school. However, as the predator moved into and through a school, the silversides split into two or more smaller groups which passed around to the sides of the predator to reunite behind and along the path just traversed by the predator. This maneuver resulted in the formation of a void or halo of clear water around the entire predator as it moved through the school. This halo was estimated to average about one to two predator body lengths in width in any direction from the predator. Similar behavior has been reported and illustrated by Breder (1959), Nursall (1973), and Radakov (1973). When a predator actually attacked, it usually dashed at high speed toward an individual in or near a school or into a segment of a school. When attacked, individuals in the immediate area of the predator jumped out of the water as they radiated out and away from the path of the predator. In a larger school, silversides at increas-

ingly greater distances from the attacking predator jumped less, the jump(s) grading into evasive swimming; and in some instances, little or no initial response was made by individuals some distance from the predator.

As jumping silversides reentered the water they realigned with other silversides that had jumped or evaded by swimming. At the same time there was a general, though somewhat belated, movement of individuals around into the wake of the rapidly moving predator. When an attack was prolonged, as when a predator chased an individual or small group of silversides, a large school often formed a number of smaller schools, which occasionally coalesced later. Frequently, jumping and/or evading individuals or segments of the attacked school joined with one or more other schools which were usually nearby but unaffected by the predator(s).

When a predator, such as a barracuda, attacked from a horizontal direction, the silversides usually had a strong lateral component to their jumps. Such jumps usually occurred at a shallow angle just above the surface and less than 45° to the surface. When attacked from directly below, initial jumps tended to have a somewhat more vertical than horizontal component, being greater than 45° to the water's surface. Distances covered during single horizontal jumps were not measured, but may have been as great as 5-10 times an individual's body length; several meters were spanned during a series of jumps.

When more than one predator simultaneously approached or attacked a school of silversides, evasive maneuvering and jumping became confused. The more rapidly increased numbers of predators approached or attacked, the more "disorganized" the silverside's evasive response appeared to become.

In Kaneohe Bay the most common diurnal predators observed attacking and chasing silversides were barracuda, *Sphyraena barracuda*; blue jack, *Caranx melampygus*; leatherjacket, *Scomberoides lysan*; and lizardfish, *Saurida gracilis*. Needlefish, *Tylosurus* sp., were also observed near silverside schools, but attacks were not seen. During the day, and particularly during the evening twilight period, the jack, *Caranx ignobilis*, may also have been a predator. This jack readily attacked silversides in field and cement enclosures. Recently ingested silversides were occasionally found in the stomach contents of

BEHAVIOR OF CAPTIVE SILVERSIDES

young scalloped hammerhead shark, *Sphyrna lewini* (45-90 cm TL), caught by gill net at night in the channels of Kaneohe Bay.

Solitary barracuda and needlefish slowly cruised along just under the surface of the water when they were near schools of silversides. When stalking, they usually remained relatively motionless as they drifted or used slow caudal fin undulations to scull along the surface. The barracuda attacked by quickly dashing, usually horizontally, a short distance towards an individual or school of silversides.

Individuals or schools of jacks and leatherjackets usually swam near the bottom in the lagoon or at some midwater depth in the deeper channels near Lilipuna Pier. Individuals of these species slowly approached or rapidly attacked the silversides, usually at an angle of about 45° to the surface. They immediately retreated towards the bottom after their approach or attack.

Lizardfish are cryptically colored, solitary benthic "sit and wait" predators. When a school of silversides swam over a lizardfish, it usually dashed at an angle nearly perpendicular to the surface, or at an angle greater than about 45° to the surface as it approached the silversides.

Because the silversides were located just under the surface of the water, the attacks by their predators could usually be detected in one or both of two ways. The momentum of a rapidly moving predator often carried it clear out of the water during an attack. This was particularly evident during attacks made in a vertical direction. If the predator turned as it approached the surface, its body and/or caudal fin usually created a boil of water at the surface, which often erupted with a popping sound into a splash or spray of water. If it was calm, a boil of water often left a small area of residual foam bubbles as concentric circles moved out across the water. When chases occurred along or near the surface, the predators often left a wake of disturbed water and froth to mark its path of pursuit.

In the Lilipuna Pier area an infrequent diurnal aerial predator was also observed. One to four common noddies, *Anous stolidus pileatus*, remained near or on the pier and flew to the areas of jumping silversides and attempted to catch them while the fish were still at the surface. Noddies were more successful at catching silversides when predatory fish attacked and then chased the silversides along the surface.

Over 100 h of observations of captive silversides in net enclosures (3 m × 3 m × 3 m deep to 6.1 m × 6.1 m × 2 m deep) in the lagoon in Kaneohe Bay and in a circular cement tank (9 m in diameter and 3 m deep with an underwater viewing window) were made during day and night periods. Within several days after introduction into the enclosures that lacked predators, the individuals in the schools of silversides slowly increased their interfish distances from less than one or two body lengths (as seen in the field) up to distances of 5-10 body lengths or more. Although the individuals were often randomly aligned with respect to each other, they did not lose their polarity to one another when a school moved. Individuals occasionally fed during the day, much as they did when free in the field. However, they did not dash out towards an object and immediately return to a school. When one or more predators, such as jacks or barracuda, were introduced into an enclosure the schools tightened as interfish distances between silversides decreased to less than one to two body lengths. Individuals continued to dart out from the relatively stationary and motionless schools, much as they did in the field. If attacks or approaches were not initiated by a predator, the schools loosened as interfish distances increased once again. These distances were not as great as they had been prior to the introduction of the predator(s). Feeding continued until approaches or attacks occurred. When approached, schools split and formed a halo around the predator as they moved to the rear of the predator to reform a school again. When attacked, individuals jumped out of the water and across the surface, away from the predator. The behavior of individuals and schools of silversides in the enclosures was much the same as that observed in the field, as described above.

During evening twilight periods, interfish distances increased as individuals in the schools spread out across the surface. During the twilight period, I could see the prey silhouetted against the evening sky, but not the predators against the bottom. As darkness increased, it rapidly became impossible to see the silversides as well, although the boils of water and splashes made by an attacking predator and the return of jumping prey into the water could be heard. During morning

twilight, interfish distances decreased as polarized schools once again formed and moved in coordinated patterns as they did in the field.

Silverside Jumping Activity Patterns

Morning Twilight

In the Lilipuna Pier area prior to nautical twilight, I could hear jumping silversides and the "pop" associated with attacking predators striking the water's surface approximately 20 min after the observation periods had commenced and 95 min prior to sunrise (Figure 1). These jumps were made primarily by individual fish in close proximity to the pier in the channel near the edge of the reef. Jumping occurred later by increasingly larger numbers of individuals in schools at the easternmost end of the observation area. Jumps occurred initially near the edge of the reef, moved toward, then turned northwest parallel to and along the shore, finally spreading out over the reef and toward the pier. These attacks by predators and jumps of silversides sequentially traced three sides of the perimeter of a rectangle defining the east, south, and west boundaries of the observed area near the pier. Attacks and jumps in shallow water over the reef predominated after the beginning of nautical twilight, and by sunrise all attacks and jumping occurred within a few meters of the pier. Peak activity in shallow reef and deep channel water was recorded just after the beginning of civil twilight and steadily decreased to midday levels (Figure 1).

The only predators observed to attack the silversides over the reef in the early morning were lizardfish. Blue jacks and barracuda were observed in the channel and occasionally over the

reef near sunrise and during the late morning.

In the lagoon area, jumps in the central deeper area of the lagoon were initially recorded 45 to 50 min before sunrise (Figure 1). As twilight progressed, jumping was eventually seen in narrow bands of shallow water along the sides of the lagoon, but occurred infrequently. Barracuda and jacks were the principal early morning predators, although lizardfish were also observed attacking the silversides. Since the shallows were relatively small in area, most of the silversides were concentrated over the central deeper water of the lagoon. A period of increased jumping activity did not occur in the lagoon during twilight as it did near the pier.

Light meter readings of 0.096-0.402 foot candle (Table 1) were made in 1973 during the time (18-24 min before sunrise, i.e., the time of civil twilight) when silversides were in the process of forming schools, especially in the lagoon area. Initial schooling became noticeable (individuals moving closer together, becoming more cohesive and polarized when swimming as they did during the day) in 1972 and 1973 as early as 44-23 min before sunrise and was completed as late as 33-18 min before sunrise (Table 2). Silversides then remained in schools throughout the day.

In summary, during the morning, predator attacks and silverside jumping could not be detected until 95 min before sunrise at the pier and 50 min before sunrise in the lagoon. Deep-water attacks were initially noted for individual silversides, but subsequently increased numbers of jumps were recorded in shallower water for increasingly larger schools, especially near the pier. During the time peak jumping occurred (30-10 min before sunrise), silversides were forming cohesive polarized schools (44-18 min before sunrise, mean 29.4 min).

TABLE 1.—Light levels (light meter readings in foot candle) and the breakup and formation of schools of silversides.

Type of activity	Author	Location	Species	Light levels		No. of readings	Remarks
				Mean	Range		
Breakup of schools	Steven 1959	West Indies	<i>Hapsita stipes</i>	0.06	0.07-0.05	2	Fish in aquariums indoor with windows and door closed, no artificial light. Watched until nightfall.
	Shaw 1961	Marine Biological Laboratory, Mass.	<i>Menidia</i>	0.12	0.35-0.03	14	Experimental; gradual reduction of light until school began dispersing. Used neutral density filters.
	This report Sept. 1973	Kaneohe Bay, Hawaii	<i>Pranesus insularum</i>	0.21	0.402-0.035	3	Field, during evening twilight.
Formation of schools	This report Sept. 1973	Kaneohe Bay, Hawaii	<i>Pranesus insularum</i>	0.18	0.402-0.096	4	Field, during morning twilight.

¹One-way analysis of variance (ANOVA) of all light meter readings ($P = 0.57$).

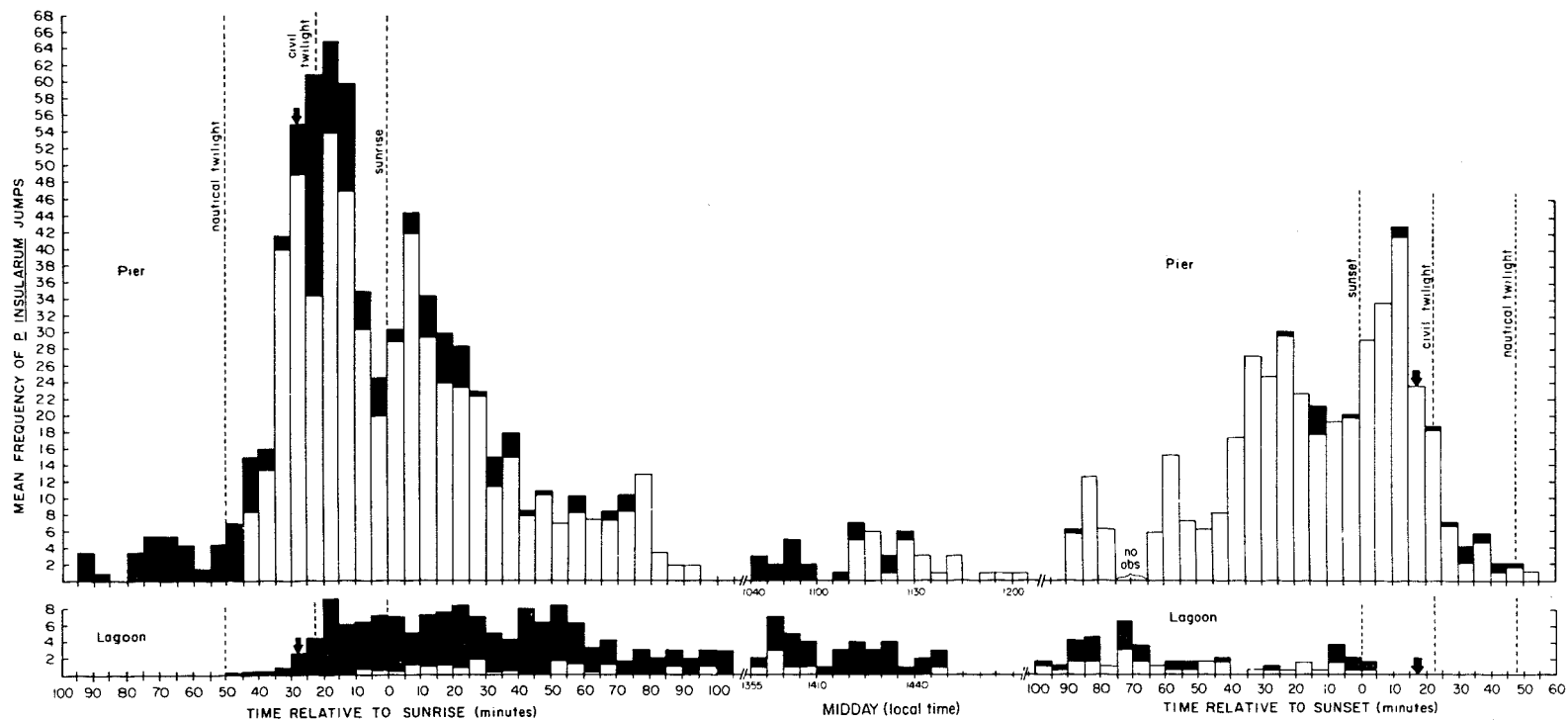


FIGURE 1.—Mean frequency of jumps (predator attacks) recorded for *Pranesus insularum* at 5-min intervals for Lilipuna Pier and HIMB lagoon areas. Times are presented relative to sunrise or sunset. Midday frequencies are presented with respect to local (real) time. The mean times of school formation in the morning and school breakup in the evening are denoted by the inverted arrows. Shaded bars denote deepwater (channel) jumps. Light bars denote shallowwater (reef) jumps. Double oblique slashes denote the breaks between morning, midday, and evening observations.

TABLE 2.—Comparison of school formation and breakup in *Pranesus insularum* with twilight phenomena recorded near Lilipuna Pier and HIMB lagoon, Kaneohe Bay, Hawaii.¹

[Mean school formation = -29.4 min (before sunrise), mean school breakup = +19.1 min (after sunrise).]

Location	Date	Local time of sunrise (h)	Relative time of sunrise	Difference in time (minutes) between sunrise and			
				Beginning nautical twilight	Beginning civil twilight	Initial school formation	Schools formed
Lilipuna Pier	7 Oct. 1972	0625	0	-48	-23	-44	-33
HIMB lagoon	8 Oct. 1972	0624	0	-47	-22	-34	-24
	23 Oct. 1972	0629	0	-48	-22	-26	-20
	19 Nov. 1972	0644	0	-51	-24	-38	-31
	21 Nov. 1972	0646	0	-51	-24	-33	-28
	22 Nov. 1972	0647	0	-51	-24	-40	-33
	12 Sept. 1973	0617	0	-48	-21	-24	-18
	14 Sept. 1973	0619	0	-48	-21	-23	-21

Location	Date	Local time of sunset (h)	Relative time of sunset	Difference in time (minutes) between sunset and			
				End of nautical twilight	End of civil twilight	Initial school breakup	Complete school breakup
HIMB lagoon	8 Oct. 1972	1814	0	+48	+22	—	+26
	22 Oct. 1972	1804	0	+48	+22	+16	—
	13 Sept. 1973	1835	0	+48	+22	—	+24
	17 Sept. 1973	1832	0	+48	+22	+15	+21
	18 Sept. 1973	1932	0	+48	+21	+14	+18

¹One-way ANOVA comparison of times of starting to school/schooling and starting to break up/complete breakup ($P = 0.004$).

Middy (1000-1500 H, Local Time)

In the pier area accurate counts of jumps made by the silversides during the time between 1000 and 1500 h local time were usually difficult to make due to waves caused by wind and nearby vessel activity.

Figure 1 presents the data collected during representative midday periods near the pier when interference was minimal. Generally, the silversides formed large elongated schools (hundreds to thousands of individuals) under or near the pier. The schools were largely inactive except when predators or potential predators such as barracuda, lizardfish, jacks, and needlefish, approached or attacked. When the tide level was low, the schools condensed and moved into deeper water near or under the end of the pier.

In the lagoon area at HIMB, the behavior and distribution of silversides was much the same during midday as it was near the pier (Figure 1). Small schools of silversides were strung out along the sides of the channel. Large schools of hundreds to thousands of fish were relatively inactive and concentrated over deeper water in the center of the lagoon. Barracuda and jacks were the most frequent predators, but lizardfish and leather-jackets were occasionally active in the lagoon.

Evening Twilight

As sunset approached, predator-prey activity increased in frequency in the pier area (Figure 1).

Peak activity occurred between sunset and the end of the period of civil twilight and then declined rapidly to stop just after the end of the nautical twilight period. The silversides moved off the reef along, but in the direction opposite to, the path taken during the morning twilight movement onto and across the reef. Attacks and jumping occurred near the pier, then out over the reef, moved eastward along and parallel to shore, finally northward to the edge of the reef at the easternmost end of the observation area. As darkness increased, attacks and jumping gradually diminished in frequency and intensity (fewer individuals in smaller and fewer schools jumped).

In the lagoon area midday jumping activity in shallow and deep water continued until just after sunset, then stopped abruptly (Figure 1). The low number of jumps in deep water in the late afternoon and evening in the lagoon contrasts sharply with the frequency of jumps in the early morning (Figure 1). This difference may be related to the low levels of incident light striking the surface of the lagoon in the afternoon and evening due to the vegetation and the mountains and clouds to the northwest obscuring the sun. In the morning the lack of high vegetation and mountains nearby to the northeast resulted in light striking the lagoon's surface so that the silverside were presumably visible to their predators.

Light meter readings of 0.035-0.402 foot candle (Table 1) were made during the time (20-24 min

after sunset, i.e., during civil twilight) silverside schools were breaking up, the individuals spreading out just under the surface of the water. In 1972 and 1973 schools began to break up (increased interfish distances became noticeable) between 14 and 16 min after sunset and were spread out by 18-26 min after sunset (Table 2).

In summary, with the approach of dusk, predator attacks and silverside jumping increased in frequency and intensity to peak during the period of civil twilight, shortly after sunset, near the pier. In the lagoon there was no peak activity; the last attacks and jumps were recorded immediately after sunset. Peak jumping near the pier was recorded 5-15 min after sunset, just before the time the silverside schools were observed to break up becoming less polarized and cohesive (14-26 min after sunset, mean 19.1). In the lagoon, however, attacks stopped before the prey schools spread out; this may have been due to the shadows and increased darkness caused by heavy vegetation along the northwest side of the lagoon.

Silverside Behavior: Conclusions

The temporal pattern of predatory attacks and silverside jumping relative to sunrise was the mirror image of that relative to sunset, at least for the Lilipuna Pier area (Figures 1, 2). For each of the four environmental situations studied, Figure 2 simplifies and graphically presents (at 50-min intervals) the mean frequency of silverside jumps illustrated in Figure 1. Midday (1000-1500 h) jumps were combined and were not divided into 50-min intervals. Statistical comparisons (analysis of variance, $P \leq 0.05$) of the jumping data for sunrise (-50 to +50 min), midday, and sunset (-50 to +50 min) for each of the four situations indicated that, at least for the shallow-water reef area near Lilipuna Pier, the frequencies of jumps at sunrise and sunset were similar and differed from the number during midday.

The mean time of school formation occurred just prior to the beginning of civil twilight in the morning, and the mean time of the breakup of schools occurred just before the end of civil twilight in the evening. Peak predator activity occurred just after schools formed (mean time) in the morning and just prior to their breakup (mean time) in the evening. The data presented indicate that related events (e.g., school formation versus breakup) occurred in the study sites significantly

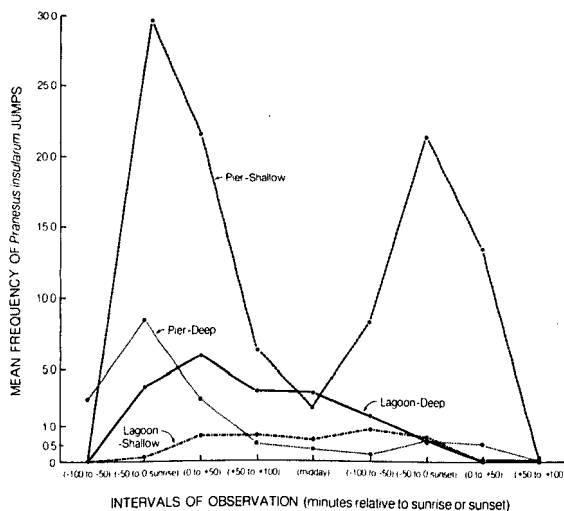


FIGURE 2.—Mean frequency of *Pranesus insularum* jumps for nine 50-min intervals (except midday). Based on data also presented in Figure 1.

earlier (about 5-15 min) in the evening, relative to sunset compared with the morning events, relative to sunrise (Table 2). This discrepancy may be due to the shadow effect of the clouds and mountains near Kaneohe Bay, which produce evening twilight conditions 5-15 min earlier than predicted, as discussed above. The relatively low frequency of deepwater attacks near the pier in the evening indicated that by the time silversides had moved off the reef and/or spread out, it may have been too dark for predators to see individual silversides. In the morning, the lack of mountains and vegetation and increasing light levels resulted in sufficient light being available for predators to see their prey.

Observations of free-living and particularly captive silversides, as well as my observations of other schooling prey species (striped mullet, *Mugil cephalus*, and Hawaiian anchovy, *Stolephorus purpurus*) in Hawaii, indicate that predation is of prime importance in shaping the behavioral patterns of prey species. When held captive in the absence of predators for days or weeks, individual prey in schools increased their interfish distances and appeared to feed more actively than they did in the field. When predators were present, interfish distances within captive schools were similar to interfish distances between individuals in the field. During the day, schooling behavior appears to serve a protective function for individuals, reducing the number of

attacks made by predatory fish. This protective function has also been observed for other schooling prey species (Radakov 1958, 1973; Neill and Cullen 1974). The chance that a predator has of singling out a specific individual silverside are greatly reduced if schools are formed. This appears to be especially true when the prey are polarized towards one another and move close together through coordinated maneuvers. In the field, when predators were not in the immediate vicinity of silverside schools, individual silversides became relatively motionless and randomly oriented towards one another, darting out from schools presumably to feed. When individual silversides presumably became exposed and/or appeared to be accessible to one or more nearby predators, the predators approached or attacked. If the predator's approach was slow, the individual silversides became polarized, the school maneuvering evasively. If a predator's approach was sudden or rapid, individual silversides jumped out of the water one or more times to evade. Both schooling and jumping presumably decrease the time a predator had to align itself with a specific individual prey. In addition, a jumping silverside often landed in the midst of its own, or that of another nearby, school, presumably disappearing from the predator's field of vision and/or path of swimming. The formation of large schools composed of many hundreds or thousands of individuals, especially a number of such schools relatively close to one another, appeared to increase an individual silverside's chance of escape when jumping.

The movement of silversides into the shallow water over reefs, and their location near and under Lilipuna Pier and heavy overhanging vegetation and along the sides of the lagoon, may be additional means, besides schooling, of reducing predation. In the shallow water near the pier, the most common vertical attacking predators were lizardfish. In deeper water in the lagoon and near the pier, jacks and leatherjackets also attacked vertically. Horizontal stalking and attacking predators, such as barracuda and needlefish, occurred in both deep and shallow water. The depth of water over the reefs may have been less than sufficient for some of the vertical attacking species to maneuver and approach schools of silversides undetected. The occurrence of silversides near structures and along the sides of the lagoon may have also limited the maneuver-

ability and avenues of approach for all species of predators.

DISCUSSION

The interactions between silversides and their predators in relation to solar phenomena are almost identical in pattern and time to those given by Hobson (1968, 1972) for the interactions of *Harengula thrissina* and their predator *Mycteroperca rosacea* in the Gulf of California. Hobson and Chess's (1973) study of the arrival and departure of *Pranesus pinguis* to and from reefs at Majuro Atoll in the Marshall Islands also showed school movement related to specific times during twilight. However, only a few predatory attacks were observed at Majuro Atoll. Comparisons of lunar and tidal changes during the studies in Kaneohe Bay and Majuro Atoll and Baja California seem to indicate a relatively minor influence on the crepuscular behavior of schools.

Hobson (1968, 1972, 1973), Collette and Talbot (1972), and Domm and Domm (1973) have demonstrated that there is relatively little activity amongst most coral reef fishes during a specific segment of the twilight period. In the morning, nocturnally active reef fish leave the open water column to hide in the coral reef approximately 30 min before sunrise (Hobson 1972). Diurnal species do not reoccupy the water column until approximately 12-16 min prior to sunrise. It is exactly between the above times, the "quiet period," as defined by Hobson (1972), that peak surface predator-prey activity and school formation takes place in Kaneohe Bay, just as it does in the Gulf of California (Hobson 1968, 1972), and possibly Majuro Atoll (Hobson and Chess 1973). The pattern is reversed during evening twilight (Hobson 1972). Diurnal reef species evacuate the water column approximately 6-22 min after sunset. Nocturnal species then reoccupy the water column about 14-34 min after sunset. Again, surface predator-prey interactions peak and schools break up in Kaneohe Bay during the time that would be comparable with the evening quiet period in other parts of the world.

The combined observations of reef fishes in the Virgin Islands (Collette and Talbot 1972), the Great Barrier Reef, Australia (Domm and Domm 1973), Hawaii (Hobson 1972), and the Gulf of California (Hobson 1968) indicate nearly identical time relationships of behavioral events during

the twilight transitional periods. This would be the predicted relationship since fish respond to specific intensities and spectral composition of light (Munz and McFarland 1973). The intensity and spectral composition of incident light at specific times relative to sunrise or sunset are identical each day, although they vary with time and season and with latitude. The amount of cloud cover and/or high mountainous terrain nearby, as in Kaneohe Bay and Kona, Hawaii (Hobson 1972) or Baja California (Hobson 1968), may shift the activity patterns to later in the morning, or earlier in the evening (i.e., shift the time relative to sunrise and/or sunset at which specific light levels occur). However, the basic relationships between behavior and twilight periods appear to hold.

Light meter readings recorded during the formation and break up of Hawaiian silverside schools are compared with those recorded for two other species of silversides in Table 1. The readings for all three species are not significantly different. Such light levels occur naturally when the sun is between -5° and -9° below the horizon during the periods of evening or morning twilight (Brown 1952). These data and the field observations reported here are also comparable to the light levels and the sun angles calculated from the data presented by Pavlov (1962) for another silverside, *Atherina mochon pontica*. Pavlov found that peak predator success occurred at light levels of approximately 0.01-108 foot candles corresponding to sun angles of -9° to $+1^\circ$ to the horizon (Brown 1952) (i.e., centered during the period of civil twilight).

These comparisons indicate that related species of silversides, which live in widely separate parts of the world, have similar visual thresholds and, perhaps, sensitivity. Munz and McFarland (1973) provided a synopsis of research, which has shown that many related species demonstrate a considerable diversity in their visual sensitivity. However, species, whether related or not, which occur in similar environments, appear to have similar thresholds and sensitivity. These relationships indicate that the above silverside species from various locations in the world may have very similar behavioral patterns and/or live in very similar physical and biological environments.

When light levels decrease in the evening, visual thresholds may be reached, making coordinated schooling movements impossible, or at least more difficult for the silversides. These thresholds

may be reached at the time when cone vision shifts to rod vision (the Purkinje shift), neither cone nor rod vision being fully efficient (Munz and McFarland 1973). As school formation breaks down or increases, the silversides appear to be the most vulnerable to predatory attack. This vulnerability may be due to reduced visual sensitivity, leading to an inability to see their predators below them against a dark bottom or deep water (Hobson 1966, 1968) and react in time to avoid and escape from them (Dill 1972, 1974a, b). In addition, such prey may be unable to simultaneously interact with conspecifics, and look out for predators at a distance at low light levels.

Predators are presumably able to see their prey at a horizontal angle or silhouetted against the twilight sky for a short period of time before their lower visual threshold is reached in the evening (Hobson 1966, 1968). Munz and McFarland (1973) indicated that increased visual sensitivity in predators, which provides sufficient resolution for the detection of prey in motion during twilight, may be a result of having relatively larger, but fewer, cones in their retinas compared with those found in diurnal fishes. This factor is critical since predators must align themselves and be able to predict where their prey will be during the mouth opening phase of their strike (Nyberg 1971).

Weighing against the hypothesis that the schools of silversides break up and reform as a result of changes in visual sensitivity, are a number of observations made of captives held in the field enclosures in the absence of predators. When held for weeks at a time, these silversides did not completely lose their cohesion and polarity, indicating that there may be a strong genetic component to their schooling behavior. This genetic component may result in the silversides remaining within a short distance of one another at all times. The silversides appear to be adapted to feeding at night as well as in the day (McMahon 1975). If they can feed at night, the silversides are probably able to detect the presence of conspecifics, either using visual and/or lateral line cues. The ability to detect conspecifics would be particularly beneficial as individuals would not become so widely scattered during the night that polarized schools could not easily reform during morning twilight. In addition, the observation that captive silversides held in large enclosures in the field in the absence of predators did not all spread out to look continuously for food indicates

that there may be a biological (circadian) rhythm related to school formation and breakup and the availability of specific food resources. Thus, the breakup of schools may reflect a preemptory predilection of individual silversides to spread out and feed rather than remain within the safety of compact polarized schools. Concurrently, predators are rapidly losing their ability to distinguish individual silversides in the fading light, but their presence remains a threat.

During the morning the process is reversed as light levels increase with predators becoming increasingly active and presumably more successful at capturing silversides. It is during relatively short daily time spans within the periods of twilight that the silversides become particularly vulnerable to certain predators. It is at these times that the silversides are passing to or from a period of feeding to a period of relative quiescence. In some areas, exposure to predators may be increased because the transition involves the movement from one location to another. The timing of such movements and the behavioral changes that occur within schools appear to be related to the threat of predation, the availability of food and the visual sensitivity and thresholds of both the silversides and their predators.

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