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Layering with depth in a heterospecific fish aggregation

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Synopsis

The schooling behavior and interspecific interactions within a nearshore planktivorous fish aggregation in Bermuda was observed during the summer (July–Sept) and winter (Dec–Jan) of 1986–87. Four species of morphologically and ecologically similar fish were studied: the silverside *Allanetta harringtonensis*, the round herring *Jenkensia lamprotaenia*, the anchovy *Anchoa choerostoma*, and the pilchard *Harengula humeralis*. Heterospecific aggregations of these fish layered with depth into discrete horizontal bands 30 to 60 cm in width. Layers were categorized by unique sets of species as well as by age of fish (measured as fish length). The median depth of the layer was also a function of whether the fish were feeding or resting. The median depth and the width of each layer were consistent across three sites and midmorning versus midafternoon observation times. Reduction in predation per individual is suggested as a possible force acting to maintain the structure of this fish aggregation.

Introduction

Heterospecific aggregations of animals have been documented in several different taxa, most commonly ungulate herds (Gosling 1980), bird flocks (Krebs 1973, Morse 1977), and in several types of fish aggregations (Barlow 1974, Itzkowitz 1977, Morse 1977, Matsumoto et al. 1984). Like a conspecific group, a mixed species aggregation may confer several types of advantages upon its members, including increased feeding capabilities and a reduction in the per capita rate of predation (Morse 1977). An increase in group size will bring about a concomitant decrease in the probability of the average group member being successfully attacked, assuming the predator(s) is satiated before the group is consumed (Brock & Riffenburgh 1960, Foster & Treherne 1981, but see Pitcher 1986). Stable heterospecific groups may offer the individual an additional advantage of more bodies to hide behind, compared to a single species grouping.

The less abundant species in a heterospecific aggregation may, however, be at a significant disadvantage in terms of predation, especially if the member species are morphologically dissimilar. Odd members that are easily picked out against a homogeneous backround have relatively high risks of consumption by predators (Hobson 1963, Mueller 1975, Wolf 1985, Landeau & Terborgh 1986). Therefore, maintenance of a heterospecific aggregation requires that its members not experience differential rates of predation, or that some other factor(s) balance the unequal detriment. If the primary advantage to the individual is a reduction in the probability of being preyed upon, then the member species should look similar. That is, differences in color pattern, body shape and behavior should be minimized such that individuals do not find themselves against a contrasting backround.

In my study, a nearshore planktivorous fish aggregation in Bermuda was examined. Found in the shallow sounds, bays, and nearshore patch reefs of the island, these fish are commonly sighted in large heterospecific aggregations in the upper half of the water column (total depth ranged from one to four meters). The five most abundant species in the aggregation were: the halfbeak, *Hyporhamphus unifasciatus* (Hemiramphidae), the silverside, *Allanetta harringtonensis* Atherinidae), the round herring, *Jenkensia lamprotaenia* (Clupeidae), the anchovy, *Anchoa choerostoma* (Engraulidae), and the pilchard, *Harengula humeralis* (Clupeidae). The last four were the primary focus of this study. Halfbeaks were not included in the analysis because they were much less abundant than the other four species, they only ate floating seagrasses (personal observation) and so were presumed not to be directly competing with the other four species for food, and finally they were not observed schooling, as did the other four species. Primarily during the winter observations the aggregation was occasionally augmented by juvenile round scad *Decapterus punctatus* (Carangidae), juvenile spottail pinfish, *Diplodus bermudensis* (Sparidae), and an unidentified clupeid, probably *Sardinella* sp.

Although phylogenetically distinct these fish are similar morphologically and ecologically. They are all small, planktivorous, silvery fish with reflective flanks which occupy vertically adjacent portions of the water column and are frequently observed in heterospecific aggregations or schools. The structure of the aggregation was documented in space and time by divers using SCUBA or snorkeling. Although no direct evidence was collected, predation seems to be the most plausible selective factor regulating the formation and continued existence of this heterospecific aggregation.

Materials and methods

Observations were conducted from July–September 1986 and December 1986–January 1987, at three nearshore locations on the north-east end of Bermuda (Fig. 1). Church Bay, Harrington Sound was rarely exposed to wind or wave action and maintained the clearest water. Richardson's Bay, Ferry Reach was subject to intermediate physical conditions. The water was usually full of suspended sediment and organic detritus making the bay turbid. Whalebone Bay along the North Shore was the most exposed to waves and surge; however, the water remained clear. All sites varied in depth from one to four meters. The bottom was mainly sand or seagrass, with occasional rocky outcroppings. At each site, half hour observations were made during midmorning (09:00–11.00 h) and midafternoon (14:00–16:00 h). Sites were visited at least five times, morning and afternoon, in the summer and at least three times during the winter. During the course of the observations school size varied over several orders of magnitude from tens to several thousand fish. With the exception of *Allanetta harringtonensis* which was always observed in small groups of 50–200, schools in the hundreds to low thousands were observed most often.

For each observation, two divers using SCUBA or snorkeling recorded the presence and placement of the four species as they occurred contiguously in the upper portions of the water column. Once an aggregation was sighted, divers remained motionless except for minor arm movement when recording data. Because of a consistent size difference and vertical depth distribution, *J. lamprotaenia, A. choerostoma,* and *H. humeralis* were recorded as juveniles or adults. There were, therefore, seven types of fish. A given fish-type could be present more than once during an observation period if more than one distinct group was observed. For each fish-type present, data were taken on their vertical range in the water column (recorded as minimum and maximum depth of the layer), and their locomotory behavior. Depth measurements were made to the nearest 15 cm by referring to a vertical transect tape suspended in the water by floats and weights.

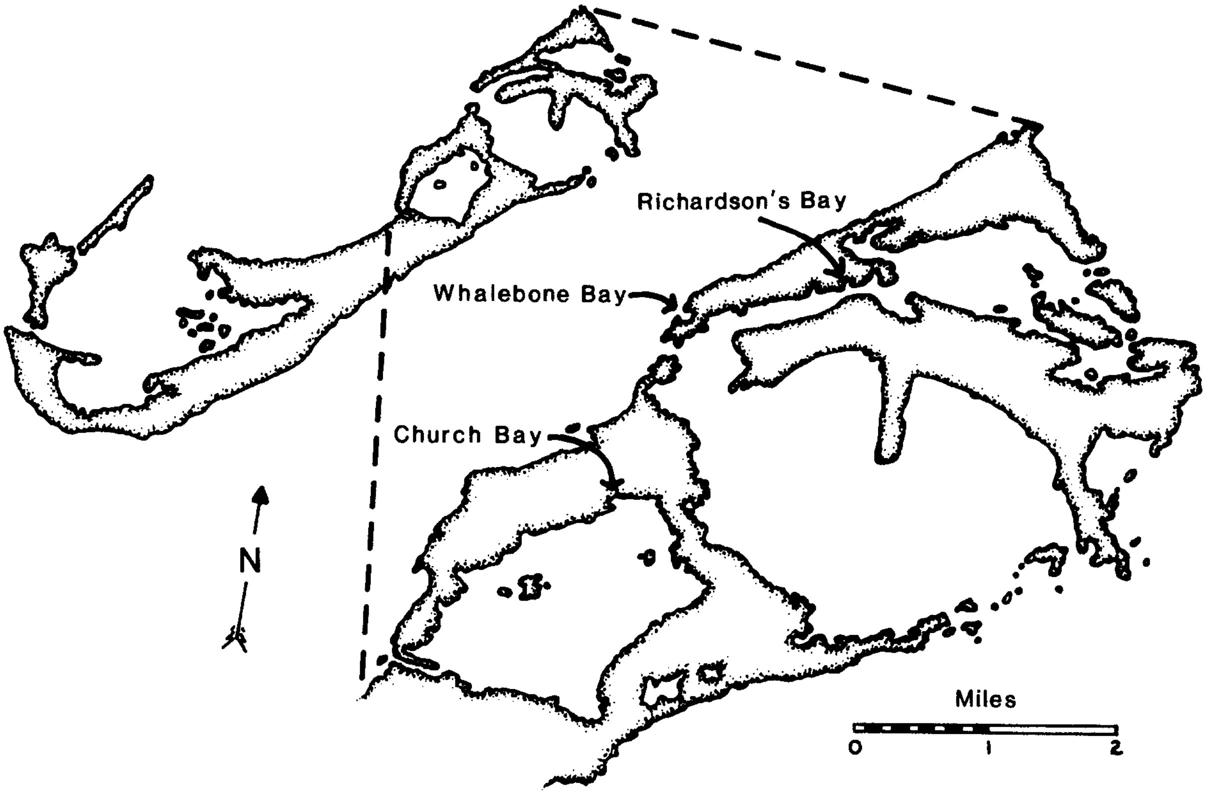

Fig. 1. Field site locations in Bermuda. Whalebone Bay on the North Shore was the most exposed to wind and wave action, Church Bay in Harrington Sound was the most protected from physical disturbance, and Richardson's Bay experienced intermediate physical conditions.

Locomotory behavior was divided into three categories: feeding, resting and swimming. Feeding was typified by a zigzag pattern of short forty-five degree (to the horizontal) darts where each individual moved independently of its neighbors. Resting fish remained stationary and, depending on the species, the school retained a polarized configuration. Swimming was further subdivided into nonpolarized (large variation in interfish distances, and/or all fish not heading in the same direction), polarized (little to no variation in interfish distance, all fish heading in the same direction) and polarized-pursued (same structure as polarized but instigated by a predator).

A given fish-type could perform more than one locomotory behavior simultaneously. In these cases a depth range was assigned to each behavior group. The vertical depth range of each fish-type exhibiting a discrete locomotory behavior was converted into a standardized median depth: median depth of the school divided by the total depth of the water column (= standardized depth). Standardized depth was used to examine a fish-type's vertical position in the water column with respect to the other fish-types present and not with respect to the bottom. Depth range for each fish-type (= maximum depth − minimum depth) was also calculated.

Water depth (m), approximate visibility (to the nearest 5 m), weather (sunny versus cloudy, and windy versus calm), and bottom type (sand, seagrass or mix) were also recorded during each observation period. Temperature and salinity (as measured by a YSI 33 S-C-T probe lowered from a boat) were recorded at 20 cm depth increments in the morning and afternoon on two or more nonobservation days, at each site. A surface layer anomaly consisting of either cold, less-saline water or

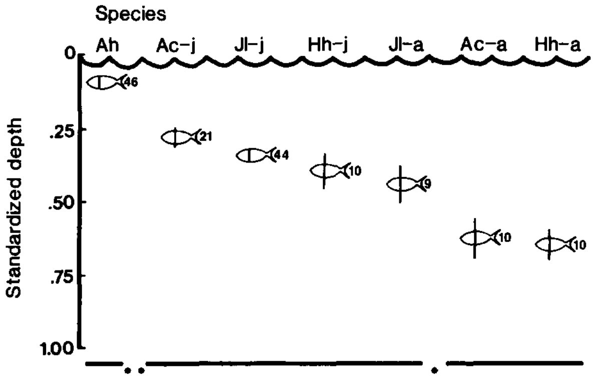

Fig. 2. Standardized depth (median depth of each observation/total depth of the water column), pooled across site, season and time of day (mean ± SE). Ah = *A. harringtonensis*, Ac = *A. choerostoma*, Jl = *J. lamprotaenia*, and Hh = *H. humeralis*. Abbreviations followed by a -j denote juveniles, while -a denotes an adult. Numbers following fish indicate the sample size for each fish-type. A Tukey-Kramer multiple range test indicates three distinct layers: Ah is the sole occupant of the surface layer, ($p<0.01$); Hh-j, Jl-j, Ac-j, and Jl-a occupy the middle layer; Ac-a and Hh-a occupy the bottom layer ($p<0.05$).

warm, more-saline water was noted, if present. These 15–20 cm deep layers reflected time since last rainfall and the relative amount of mixing at each site.

Determination of fish standard length was made by measuring ten juveniles and ten adults of each species. The fish were provided by a local bait fisherman, or netted with a beach seine at the Richardson's Bay site.

Standardized depth and depth range were averaged across each fish-type, by locomotory behavior. Analysis of variance (ANOVA) was used to determine whether fish-types occupied unique horizontal bands and whether the standardized depth of each band was significantly influenced by locomotory behavior and/or in response to physical characteristics of the habitats. Tukey-Kramer multiple range tests were used to determine which standardized depths and ranges, by fish-type, were distinct. A least-squares regression was used to determine how well standardized depth was explained by standard length.

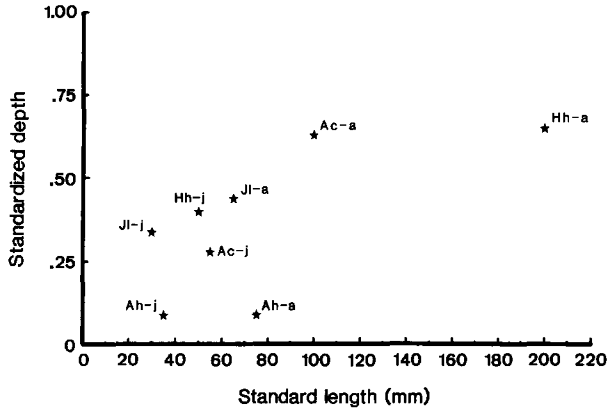

Fig. 3. Size, measured as standard length, of each fish-type regressed against standardized depth. $Y = 0.003X + 0.167$, $r^2 = 0.45$. Each * represents a mean of 10 fish. See Figure 2 for abbreviations.

Results

Fish layered with depth by fish-type (Fig. 2 – $p<0.001$, one-way ANOVA). Site, and observations in winter versus summer, as well as during midmorning versus midafternoon did not have a significant effect on the standardized depth of any fish-type ($p = 0.84$, $p = 0.10$, $p = 0.74$, respectively, one-way ANOVA); therefore the results were pooled by fish-type. A Tukey-Kramer multiple range test indicated three distinct layers. The surface layer was always occupied by *A. harringtonensis*. The middle layer was composed of *J. lamprotaenia* juveniles and adults as well as juveniles of *A. choerostoma* and *H. humeralis*. *Harengula humeralis* juveniles were usually observed as singletons or in small discrete schools (5–30 individuals), within the main body of the middle layer. The lowest layer was occupied by *A. choerostoma* and *H. humeralis* adults.

Body size partially accounted for the observed stratification (Fig. 3), although the linear regression fit is weak ($r^2 = 0.45$). In general, smaller fish occupied higher positions in the water column than larger fish. Locomotory behavior had a highly significant effect on standardized depth (Fig. 4 – $p<0.001$, one-way ANOVA). All species ate above where they rested with the possible exception of *A. choerostoma* adults which were never

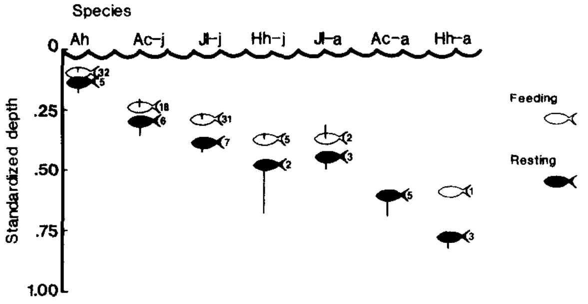

Fig. 4. Pooled standardized depth of each fish-type by locomotory behavior (mean + or − SE). Locomotory behavior is divided into feeding (white) and resting (black). Numbers following fish indicate the sample size for each fish-type. Adult *A. choerostoma* (Ac-a), were never observed feeding. See Figure 2 for abbreviations.

observed feeding. There was no effect of swimming on standardized depth ($p>0.34$, one way ANOVA). When swimming, all fish-types swam in each of the three swimming patterns regardless of the depth they occupied.

Average depth range was not significantly different between fish-types (Fig. 5 – $p = 0.07$, one-way ANOVA), although a Tukey-Kramer multiple range test indicated that the average range of *H. humeralis* was significantly larger than all other fish-types ($p<0.05$). With the exception of adult *H. humeralis,* each fish-type occupied approximately 40 cm of vertical space. Adult *H. humeralis* are at least twice as large as all of the other observed fish-types, therefore their larger average range may have been strictly an effect of their body size.

All seven fish-types were only occasionally found together. Usually, two to four fish-types were observed in an aggregation. Both homotypic schools and the entire heterospecific aggregation were rarely observed. Because the middle layer was composed of four fish-types, a physical gap in the aggregation was never observed. Absence of the top or bottom layer did however, shorten the vertical depth range of the observed aggregation as a whole, so that it did not reach the surface or below midwater, respectively. Standardized depth of any fish-type was not affected by the presence/absence of other aggregation members ($0.69>p>0.21$ in every case, MANOVA).

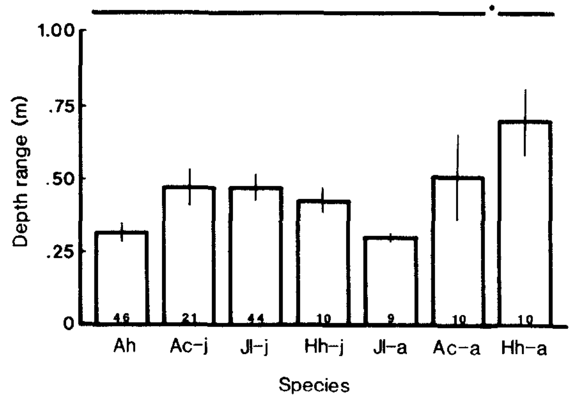

Fig. 5. Depth range of each fish-type pooled across site, season and time of day (mean ± SE). Numbers inside bars indicate the sample size for each fish-type. A Tukey-Kramer multiple range test indicates that all fish-types have equivalent ranges (approximately 40 cm) except *H. humeralis* which has a significantly larger range ($p<0.05$). See Figure 2 for abbreviations.

Weather and bottom type did not explain the observed stratification ($p>0.14$, one-way ANOVA, in every case). Temperature and salinity remained almost constant over the 1–4 m depths tested (greatest temperature range = 2° C; greatest salinity range = 2 ppt), with the exception of the surface layer which was solely subject to minor fluctuations (±1.5° C, ±2 ppt).

Discussion

Presence and absolute abundance of each fish-type differed between sites and between the summer and winter observation periods; however, the horizontal stratification pattern in the aggregation remained constant. None of the physical factors that were concurrently measured had an appreciable effect on the standardized depth of any fish-type. Presence/absence of the other members of the aggregation seemed to have no effect on the standardized depth of each fish-type. However, not all combinations of fish-types were observed and repeated observations of other combinations were low. Thus it was hard to distinguish any clear effect that may have been present.

The structure of the aggregation into horizontal bands is a function of fish-type, and locomotory behavior. In general, small fish occur higher in the water column than larger fish (Fig. 3), a phenomenon that has been previously recorded in several diverse habitats (Yuen 1962, Brandt 1986, Brewer & Kleppel 1986). In addition, each fish-type feeds above where it rests (Fig. 4).

Discrete layering by species within a community along some spatial axis is not uncommon. Rocky intertidal communities exhibit distinct horizontal striations as a result of physiological range and interactions between the member species (Underwood & Denley 1984). The vertical range of several freshwater fishes is well correlated with physiological preferences for temperature, oxygen concentration and light intensity (Engel & Magnuson 1976, Rudstam & Magnuson 1985). These latter ranges however, span tens of meters, not the 20–50 cm observed in this study. Yuen (1962) reports possible monospecific layers (2–3 m in depth) within an aggregation of yellowfin tuna, *Neothunnus macropterus* and skipjack tuna, *Katsuwonus pelamis*, with the smaller skipjack occurring above the larger yellowfin. He hypothesized that monospecific schools were brought together by common food sources.

Several references to mixed species schools of similar-looking planktivorous fish have been made in the literature. Springer (1975) mentioned several species either netted together, observed with closed circuit television, or observed schooling in onboard tanks. These fish included *J. lamprotaenia*, and unidentified anchovy, several species of *Harengula, Decapterus punctatus* and *Sardinella anchovia.* Hobson (1963) detailed discrete subschools of the anchovy *Cetengraulis mysticetus* moving among a much larger school of *Harengula thrissina,* the flatiron herring. In both cases however, discrete layers were not described. Sympatric *Notropis* species have been shown to distribute themselves with depth as well as along a longitudinal cross-section in shallow creek pools (less than one meter in depth) in accordance with their preferred food supply (Mendelson 1975). However, the data result from trapping and the author was unable to use direct observation to determine whether the aggregation was composed of conspecific layers.

Within the aggregation, the four species differed minimally in morphology. Inexperienced divers frequently mistook one species for another, and even experienced divers had to approach the fish quite closely (less than one meter for fish less than 50 mm in standard length), to make positive identifications. Predators may experience the same difficulty. If this is true, no one species in the aggregation should suffer a higher risk of predation due to recognition by the predators than any other, given equal numbers of each species (see points 1 and 3, p. 1378, Landeau & Terborgh 1986).

If predators are able to detect morphological differences, the individuals at the layer boundaries may be at greatest risk simply because they are closest to individuals differing morphologically from themselves. One would therefore expect these outer fish to move towards the center of their conspecific school (Hamilton 1971), leaving a physical gap between the species. Alternatively, one might expect to see a more heterogeneous mixing instead of the maintenance of discrete layers. Neither alternative was the case in my study. However, lone *H. humeralis* and *A. choerostoma* juveniles observed swimming in the middle layer during predatory onslaughts frequently swam in fast distressed bursts not necessarily in the general direction of forward motion (personal observation, see also juvenile *Sparisoma viride* behavior in mixed species aggregations, Wolf 1985).

While all observed species are similar morphologically, individual fish are probably at less risk in a group of conspecifics than in a group of heterospecifics, especially as loners. Individuals who stray from their conspecific core into the next horizontal band may be left behind if their conspecifics leave the area en masse. Schooling planktivorous fish often leave the relative safety of their diurnal shallow water locations to feed in deeper water at night (Hobson 1968, Major 1977). Occupying different layers may also allow these fish to make use of different food sources (see Mendelson 1975). This Bermudian nearshore plantivorous fish aggregation may be an example of potential competitors providing each other with associational defenses against a common threat.

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