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Visibility as a factor in the copepod-planktivorous fish relationship

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SUMMARY: The question we treat in this contribution is whether or not planktivorous fish can use the motion pattern of planktonic copepods to distinguish these animals from other suspended particles in the water. A targeted overview of the predator-prey relationship is followed by a first report of experiments performed in our laboratory where fish selected between two virtual targets on a TV screen, each target showing a different swimming pattern. The results suggest that fish can perceive temporal visual patterns and select their preferred target after two to ten seconds observing the two moving targets. Implications of these preliminary results are discussed and hypotheses for further research formulated.

Keywords: visibility, planktivorous fish, zooplankton, calanoid copepods, *Daphnia*, predator-prey relationship, temporal pattern recognition, random flow.

RESUMEN: LA VISIBILIDAD COMO FACTOR EN LA RELACIÓN COPÉPODOS-PECES PLANTÍVOROS. – En este trabajo hemos estudiado la capacidad de los peces planctívoros para detectar las trayectorias de los movimientos de los copépodos y para distinguirlas de trayectorias generadas por otras partículas. Una revisión de las relaciones depredador-presa precede la descripción de experimentos realizados en nuestro laboratorio. En estos experimentos el pez seleccionó entre dos trayectorias virtuales diferentes en una pantalla de televisión. Los resultados indican que el pez puede percibir visualmente tendencias temporales y seleccionar sus presas después de observar los movimientos de éstas durante unos segundos (2-10 s). En este trabajo se discute la implicación de estos estudios preliminares y se plantean hipótesis para futuras investigaciones

Palabras clave: visibilidad, peces planctívoros, zooplancton, copépodos calanoidos, *Daphnia*, relaciones depredador-presa, reconocimiento de tendencias temporales.

INTRODUCTION

The Academic Press Dictionary of Science and Technology (Morris, 1992) defines "Visibility: (1) the state or fact of being visible; (2) the relative ability to be seen under given conditions of distance, light, atmosphere, etc.; (3) *also called Visual Range*, the distance at which a given standard object can be seen and identified with the unaided eye; (4) the ability to give a relatively large range of unobstructed vision; and (5) *in Typography* legibility." The *North American Lake Management Society* adds at their website that visibility is "the distance to which an observer can distinguish objects from their background. The concept may apply to both air and water. The determinants of visibility include the characteristics of the target object (shape, size, color, pattern), the angle and intensity of sunlight,

the observer's eyesight, and the extent of light absorption and scattering caused by air and water contaminants." Visibility-air travelers hear the word every time the flight crew informs them of the weather conditions at the destination of the flight, and every SCUBA-diver has experienced that visibility under water is far less than in air. In clear ocean water objects at about a distance of 30 meters vanish from sight.

The definitions of visibility show an intriguing range of complexity. Let's assume a predator-prey relationship. On one side is the prey—if ever possible to not be visible at all. However, the same holds true for the predator—the prey should not see it and most predators have their own predators. The distance between the predator and its prey should be short enough for the predator to capture the prey but large enough for the predator to have a high probability of encountering a prey (Gerritsen and Strickler, 1977). Between the predator and the prey the environment could have a uniform character, or it could be of a complex nature. For a prey, the strategy of not being seen in a uniform environment would be to keep a great distance from the predator in order to be of an apparent size below the resolution of the predator's eyes. In a complex environment the prey would in size, shape, coloration and pattern match the complexity of the environment in order not to "stand out".

We will focus, here, on a very challenging case. Small fish prey on planktonic copepods. For our case these small fish live either within a complex coral reef environment or within the uniform blue waters of the upper pelagic ocean environment. In either event they have to perceive the prey item, approach it without stimulating it to perform an escape reaction, and capture it before another planktivorous fish gets it first. Considering the watery environment, planktonic copepods—the prey—should evolve into the least visible animals. Most are as transparent as they can be. However, within their immediate environment other particles may be suspended and so one could somehow "hide" among them, if one would behave as these particles behave. For fish this means that one would have to discriminate between suspended copepod "particles" and all other suspended particles. An energetically costly strategy would be to attack and capture every particle and spit out the non-desired ones. One would not only waste energy in capturing and spitting-out the useless particles, one would also forfeit all encounters with real food particles during that time interval.

Let's focus on the notion that zooplankton could "hide" among the other suspended particles. These particles would not sit still within the water column. They are entrained in the flow system of their environment and, since water is only still and motionless when frozen, all these particles will move. Two neighboring particles may move "in tandem", parallel directions and at the same speed. However, most likely there would be a difference between them, and as the turbulent dissipation rate increases, a more complex temporal picture of the suspended particles within a given water volume develops. To "hide" within such a volume would mean for a copepod to behave as "they" behave, randomly and unsteady, with a pattern complexity matching "theirs".

However, planktonic copepods have to feed as well. To behave totally randomly and unsteady may not be the best strategy to capture food, especially at low food densities. Hence, there may be a compromise to be found over evolutionary times: behave, swim, change speed and direction so that at a larger distance one looks like just a suspended particle. However, at a shorter distance, the size of the feeding current, one needs several versions of feeding currents so that one can adhere to a certain complexity of an overall motion pattern.

For the planktivorous fish the problem becomes tactically a tricky one. There is only a short time interval between encountering a particle, perceiving it as a desired one, attacking and capturing it. We were made aware of this problem when we viewed videos of fish behaving on a coral reef. We videotaped their behaviors in Kenting, Taiwan. The water moved over the corals at a speed exceeding one meter per second. The damsel fish moved only about one meter away from their "home" coral, dashed up and down, forth and back, and captured as many copepods as they could, but never spit out any non-food items. How did the fish decide what is food and what is not in the very short time interval between the prey entering the encounter range and consequently being attacked?

Here we will review results from research by others, as well as report on research we have conducted, which will lead to answers and hypotheses about how visibility influences the predator-prey relationship among the fish-zooplankton interface. Needless to say, that we cannot review all the literature and, therefore, only mention the ones most conducive and familiar to us. Our intent is to formulate hypotheses which have to be tested and, therefore, may not hold up under the scrutiny of vigorous experimentation.

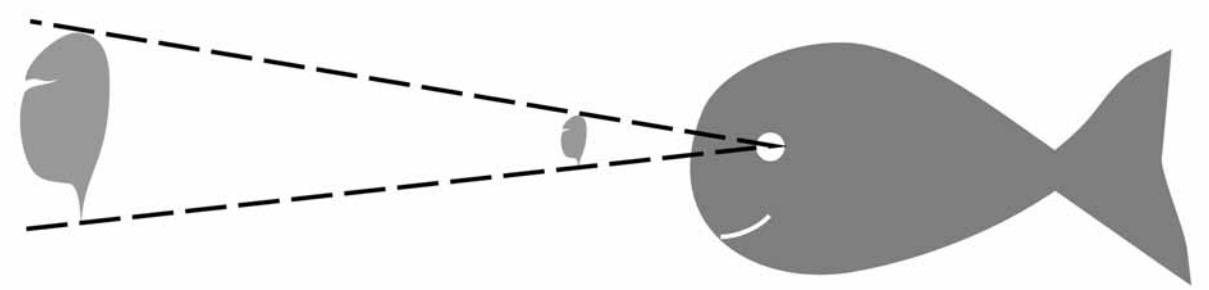

FIG. 1. – Schematics of the concept of apparent size. Large but far targets may have the same stimuli strength as small and near ones.

HOW DO FISH SELECT FOOD?

The process by which a predator selects its prey provides the driving force behind all trophic cascades (O'Brien *et al.*, 1990). Visual cues are an important factor in this predator-prey relationship (Curio, 1976). In aquatic ecosystems, selective visual predation by planktivorous fish has greatly affected the composition of zooplankton communities (Brooks and Dodson, 1965). Several models have been constructed using the components of the predation cycle—search, encounter, pursuit, and capture—and optimal foraging strategies to analyze fish predation and its impact on zooplankton populations (Werner and Hall, 1974; Confer and Blades, 1975; Egger, 1977; Zaret, 1978). According to these models, planktivores make selections based upon numerous visual factors, including size, visibility, color, shape, and motion (Ingle, 1971; Ware, 1973; Egger, 1977; Li *et al.*, 1985; Gerking, 1994).

Numerous investigators have shown in areas with greater prey density, planktivores selectively prey upon larger zooplankton. Brooks and Dodson (1965) attribute this selectivity to the greater visibility and higher energy content of larger prey. Zaret (1972a, b) and Zaret and Kerfoot (1975) confirmed that greater visibility results in greater predation; the amount of body pigmentation in zooplankton proved more important than overall body size in prey selection by fish. Furthermore, O'Brien *et al.* (1976) determined bluegill sunfish (*Lepomis macrochirus*) selected the prey that appeared largest, either because of its actual size or proximity to the fish, represented in Figure 1. Apparent size selection has been confirmed in several fish species, including lake trout (*Salvelinus namaycush*), brook trout (*Salvelinus fontinalis*), and white crappie (*Pomoxis annularis*) (Confer *et al.*, 1978; O'Brien, 1979; Wright and O'Brien, 1982).

By investigating the distance at which fish behaviorally demonstrate a recognition of prey, the reactive distance, the factors affecting selection can be studied. The reactive distance of several planktivores to a variety of prey species has shown to increase linearly with prey size (Confer and Blades, 1975; Kettle and O'Brien, 1978; Wright and O'Brien, 1982). Figure 2 shows the linear regression of reactive distance to prey size for moving and non-moving *Chaoborus* spp. and to *D. magna*.

Zooplankton swimming motion is an important factor altering predation rates; motion can distinguish one species from another and prey from non-prey. Ware (1973) showed rainbow trout (*Salmo gairdneri*) to locate moving targets 74% more successfully than visually identical objects at rest. In a study of a natural lake setting, Zaret (1980) found

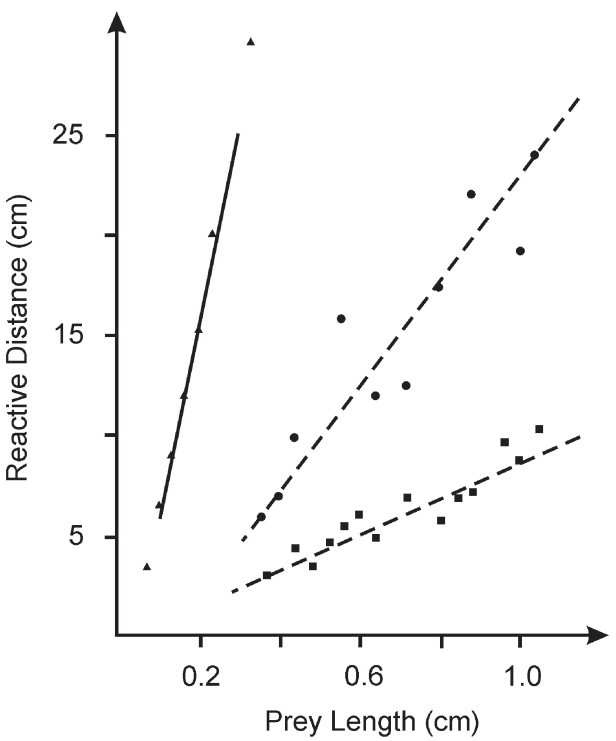

FIG. 2. – The reactive distance as the dependant of prey length and whether or not the animal is moving. Dashed lines are from *Chaoborus* spp., the solid one from *Daphnia magna*. in *Chaoborus* spp. the dots represent data from moving animals, the squares the non-moving ones. (Redrawn from Wright and O'Brien, 1982).

that fish preferred *Bosmina* to two other *Bosminidae* species even though it had the smallest mean body size and eye pigmentation diameter. He concluded that prey motion was more influential than size, or contrast, in prey selection and that fish may be using a "search image" of prey motion to locate prey. Brewer and Coughlin (1996) contrived a Virtual Plankton (VP) system using computer-generated images whose size, shape, color, and swimming behavior can be controlled to observe fish predation. Bluegill sunfish, given two VPs of varying speed, were shown to prefer the faster VP significantly to the slower moving VP. A lack of investigation in marine predator-prey relationships yields no data pertaining to prey selection, we can only suggest that the visual factors outlining freshwater selection are consistent with saltwater selection.

HOW DO FISH CAPTURE COPEPODS?

Once the fish has selected its target from all the suspended particles and food items the challenge arises of capturing the particle. Copepods are especially adept in escaping an attack. Drenner *et al.* (1978) conducted experiments using a suction device within an aquarium as an artificial "predator". A horizontally fixed tube had the diameter of a fish's mouth and "sucked" a fish's volume of water within the same time frame as a fish would do. When a particle of interest sank or swam into the volume in front of the tube a mechanism was triggered to capture the item. The distance between the edge of the tube and the position of the particle was observed as well as whether or not the particle was captured.

As particles of interest, a variety of live planktonic micro-crustaceans populated the aquarium; some were cladocerans, some copepods. To get an idea of how a non-behaving particle would get caught, oil droplets of the same specific gravity as zooplankters and heat killed zooplankters were released above the test volume and the suction was triggered when these particles sank in front of the tube. The results show clearly that copepods are much more capable of avoiding capture by the suction device than cladocerans (Fig. 3). The authors went further and defined the area under the curve of the bubbles as 100% capture probability by the device. The tested copepods' area was much smaller and their capture probabilities hovered between 7% and 24% (Fig. 3; see Drenner *et al.*, 1978).

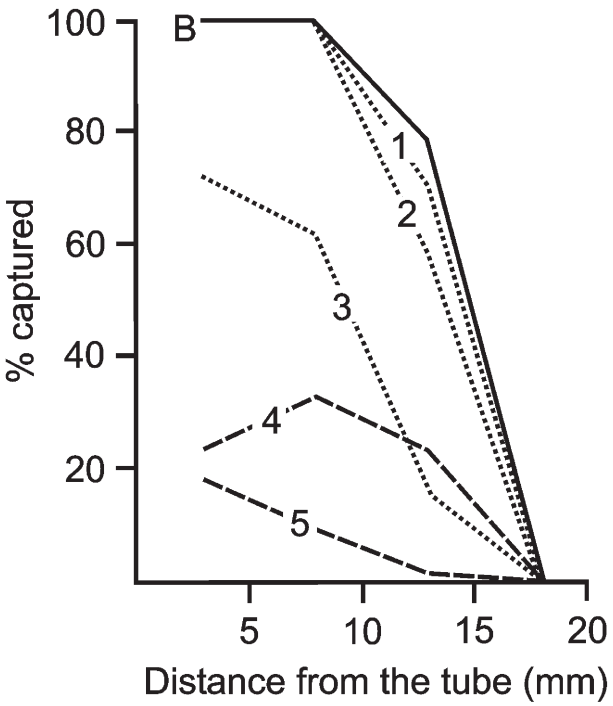

FIG. 3. – The capture probability of being captured at a distance from a simulated predator fish. (B) oil droplets and heat-killed zooplankters, (1) *Ceriodaphnia retuculate*, (2) *Daphnia galeata mendotae*, (3) *Diaphanosoma brachyurum*, (4) cyclopoid copepods, and (5) *Diaptomus pallidus*. (Redrawn from Drenner *et al.,* 1978).

These and other observations on the same topic stimulate new questions. How can copepods avoid being captured? What kind of an escape reaction are the copepods performing? What are the signals triggering an escape reaction? Again, experimentation will help us to find solutions. The sizes and swimming speeds of copepods give us a hint. With speeds around 1 to 10 mm s^{-1} and sizes in the range of 0.5 to 10 mm, copepods swim at Reynolds numbers of 1 to 100. This means their environment is viscous. In such a sticky environment anything small moving will move with a relative large amount of water attached to it. In other words, the boundary layer is relatively large. Additionally, setae stretched out into the water volume around a copepod are "stuck" in that water; any movement of the water near-by will move the setae. Now let's set up the experiment. If we release from a pipette a small amount of water it will "push" water around as would an approaching animal or a sucking fish. This pushing around water will influence the water close to the animal; its setae will be bent and the animal will receive a signal.

Years ago, Strickler (1975) not only set up such a pipette system but also a Schlieren optical system for observing the subsequent behavior. Escaping

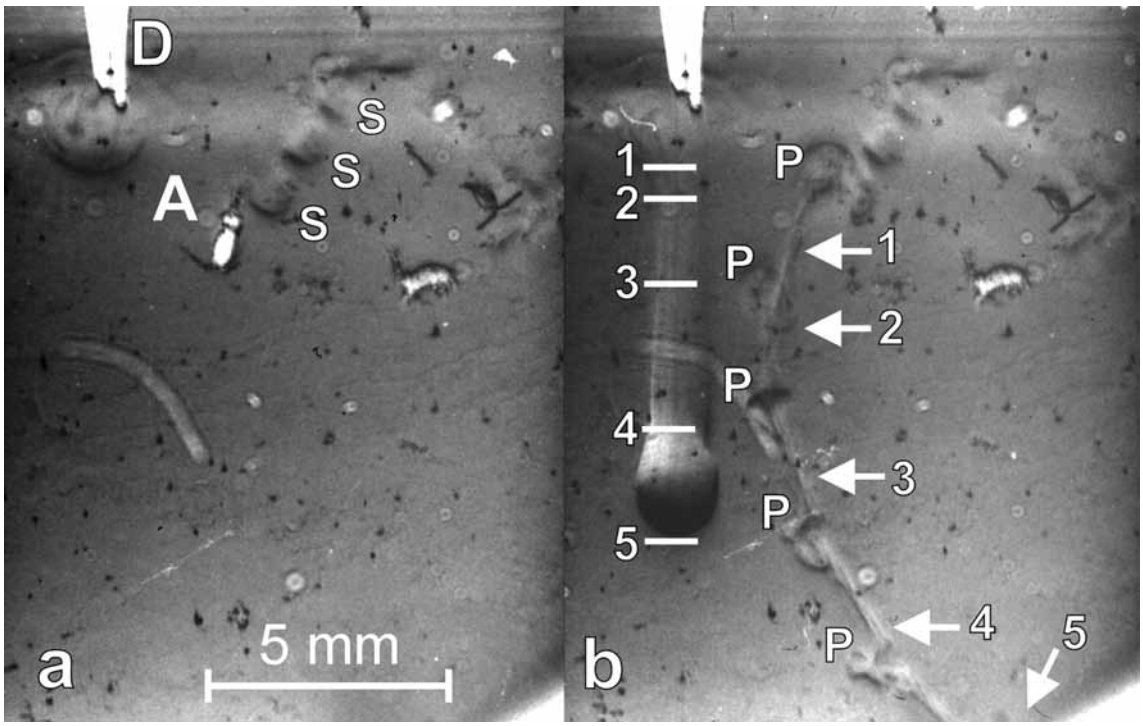

FIG. 4. – Escape reaction of *Cyclops scutifer*. (a) The female Cyclops (A) passes after swimming strokes (S) the pipette (D), which will generate a disturbance simulating an attacking invertebrate predator. (b) Positions of the distrubance (2) 0.021 sec, (3) 0.042 sec, (4) 0.063 sec, (5) 0.084 sec after (1). Positions of animal at the ssme times. (P) Position of power strokes by the swimming legs to escape from simulated predator. Escape speeds of the animals can be up to 1,000 body-lengths per second for the duration of a few seconds. (Data from Strickler, 1975).

copepods do so at great speeds. However, if they swim through a slight density gradient they will disturb the gradient, and the Schlieren system will allow observation of the swimming tracks—the foot prints—even if observation of the animal cannot be registered due to high speed of the swimming performance (Fig. 4).

Figure 4 shows several results. One, the animal veered away from the source of disturbance. Therefore, it had positional information about the disturbance. Two, the disturbance entered the water column because while being pushed out of the pipette it had kinetic energy which needed to be transformed first. Pushing the water volume out of the pipette at different speeds created disturbances with more or less penetration into the water column. This was then answered by the animal with more or less vigorous escape reactions. Therefore, the animal perceived the temporal character of the disturbance. Three, the speed of the animal, about 500 body-lengths per second, allowed the animal to use a "Dolphin kick" with the abdomen at double the frequency of the motion by the swimming legs. Therefore, the animal made use of the changing flow system around it which changes from a low-Reynolds number flow to a medium-Reynolds number flow where inertia starts to have an impact. Similar results were obtained by Buskey and Hartline (2003). Their animal, *Acartia tonsa*, was observed with a high-speed video camera. These researchers found that their animals reacted to the stimuli within four milliseconds—an extremely fast reaction time. These escape jumps were executed at maximum speeds of over 800 mm s^{-1} with maximum accelerations of over 200 m s^{-2}.

Lately a good amount of research has been conducted on the topic of escape reactions. One could enter the following author keywords in search engines and find the literature; Buskey, Davis, Fields, Hartline, Kişrboe, Lenz, Visser, Yen, and many others. Common to all results is that planktonic copepods are equipped with one of the best escape system among invertebrates. This statement primes the next question: how can a fish capture a copepod? There are some planktivorous fish that survive on a diet of mostly copepods, among them especially are coral reef fishes that feed on calanoid copepods (e.g. Emery, 1973; Hobson, 1974; Hobson and Chess, 1976).

To observe small fish capturing calanoid copepods necessitates an experimental set-up which has a time resolution of two milliseconds and a spatial

resolution of only 15 micrometers. One would like to see the fish's mouth and its movements. One needs to see the copepods and their reactions. Additionally, one should see the algae around the scene in order to use them as tracers of the flow during the capture. Without all three targets in one series of pictures it would be hard to figure out whether or not the fish sucks a volume of water into its mouth—a volume which includes the non-aware food item. Or, the fish could "pick" the food item without disturbing the water volume around the food item—if the algae did not move this interpretation would be correct.

The optical set-up Coughlin and Strickler (1990) used had the matching spatial filter design of Strickler and Hwang (1999). A Krypton laser at 1 W of light energy was used and the exposure time of each frame was 55 microseconds at 500 frames per second. Some observations were made at 100 frames per second in order to extend the observation time from six to thirty seconds. Figure 5 is a typical result made at 100 frames per second. The copepods were carefully released from a pipette above the observation volume; they started to feed and to move into the volume. These copepods were the only prey animals in the aquarium. The fish was trained to attack on signal. Trials without the expensive film in the camera were used to condition the fish that when the noise from the camera starts it is time to attack.

The experiments show that the fish protrudes its jaw and captures the food particle with a ram-jaw feeding strike as reported by Davis and Birdsong (1973). During such a strike the algae within the volume did not move; therefore, there was no suction involved. The prey was "picked" from the water within 4 milliseconds (see Fig. 2 in Coughlin and Strickler, 1990). Remarkable is that the strike time of four milliseconds matches the reaction time as reported by Buskey and Hartline (2003). The speed of the strike is fast enough that we never observed a successful escape in the many experiments during fine-tuning the experimental procedures.

The reason for not sucking any water into the mouth becomes clear when we analyze Figure 5. In the situation leading up to the observations we loaded four copepods into the pipette and released them one on the top of the other (Fig. 5a). For whatever reasons the fish targeted the second lowest animal as its first prey (Fig. 5b), and struck it (Fig. 5c). The two animals near-by perceived the slight motion of the water due to the protrusion of the jaw and escaped. The protrusion is executed at high speed which means that

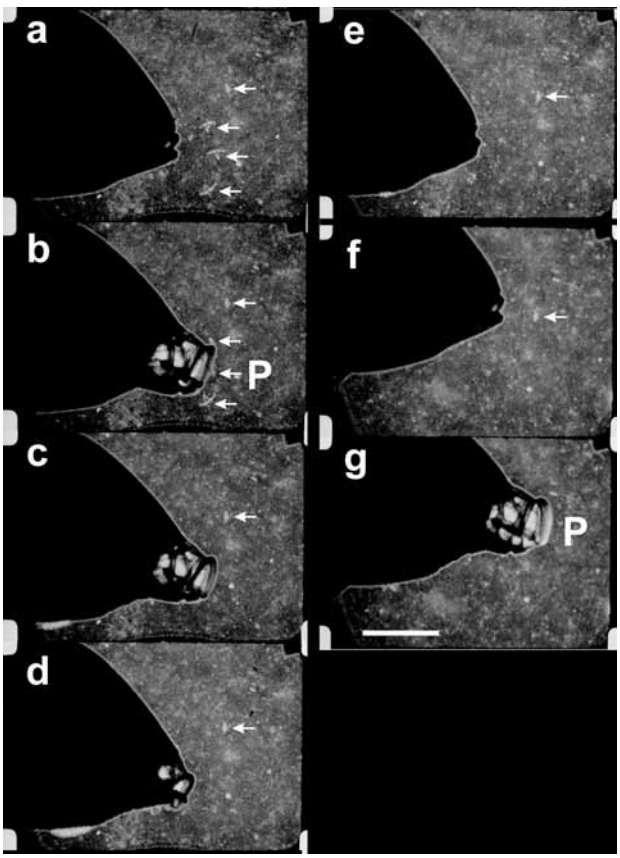

FIG. 5. – Selected prints from 16 mm film (100 frames per second) of two feeding strikes by *Chromis viridis* on calanoid copepods, *Eucalanus crassus*; bar = 1 cm. (a) The fish selects one copepod from a group of four at 0 msec. (b) After 10 msec the fish initiates a feeding strike. (c) By 20 msec it has captured the first copepod. Two of the four copepods have escaped with evasive reaction, leaving only one at (d). (e) The fish has repositioned 790 msec after (a) and captures the remaining copepod at 800 msec (f). (from Coughlin and Strickler, 1990).

the boundary layer is relative small; only near-by animals would perceive it. The forth animal did not perceive the imminent danger and in less than a second was caught as well (Fig. 5g).

This type of picking a prey from the water is a highly precise action. The prey, free-floating in the water and swimming at the same time as a self-propelled body, has to be brought within the strike volume in front of the mouth. The fish itself is also free-floating and self-propelled. Additionally, the water volume that both animals are a part of is moving and mixing. In the short time available to the predator only visual cues will be transmitted instantly. Chemical cues will undoubtedly be so mixed due to the ambient random water flow that precision is not given. We tested preliminarily the question whether or not mechanical information is necessary for the predator to locate the prey and to position itself so that they prey is within the strike volume.

We constructed a real image hologram of a calanoid copepod. In real image holograms the generating laser beam shines through the hologram from behind and produces a calanoid some distance in front of the hologram. We placed the hologram close to the aquarium and moved it in a collimated laser beam in such a way that the real image calanoid is lowered from the pipette into the water in the same fashion as the real animals mentioned above moved. The fish attacked the hologram with the same vigor and precision as the real animals. This means, since holograms are only optical illusions and do not produce mechanical disturbances in water, the visual cues the fish received provided enough information for the execution of the attack. In short: visibility is, at least between these animals, the decisive factor in the outcome of the predator – prey interactions.

DO COPEPODS SWIM AT RANDOM?

From above we can conclude that the "arms race" between the predators, planktivorous fish, and the prey, planktonic copepods, has found its ultimate barriers. The execution of a feeding strike in four milliseconds matches the escape reaction of four milliseconds. Hence, the copepods would have to resort to other measures in advance of the feeding strikes to lower the predation rate. Let's go back to the example we mentioned earlier where a strong flow bring copepods across the coral reef environment and the fish hover above the corals and attack one zooplankter after another.

The fish hide among the corals as soon as danger appears. They will venture from their hiding space one to two meters to forage, ever ready to dash back into the corals. With an ambient water flow of about one meter per second the fish has about one to two seconds time to perceive a food item, position itself for the precision attack, and strike. The visibility of water in this environment does not allow the fish to recognize details of the prey's morphology. There are simply too many suspended particles around that scatter the light and make perception of high frequency optical information unreliable, even if the eyes could perceive the fine details of copepod structures. Therefore, a copepod is a particle in the water just as much as the suspended detritus and marine snow are particles in the water. How then can a fish sort these particles? An even more intriguing question would be: do planktonic copepods swim in such a fashion that they mimic suspended detritus? At least, seen from a meter or so the copepod should be indistinguishable from a dead particle.

Strickler (1969) observed about 50 cyclopoid copepods swimming in a five-liter vessel. The ambient light had an irradiance of 0.05 to 50 erg cm^{-2} s^{-1}. The animals were observed with near-infrared light for over two hours at the time. For our arguments here two results are of interest. One, the animals reacted to a moderate change of light intensity. And two, during small changes of light intensity or none they seemed to swim in a random fashion. Let's look at these two situations in more detail.

Figure 6 shows the swimming pattern of one animal. For 180 seconds the animal swam within a

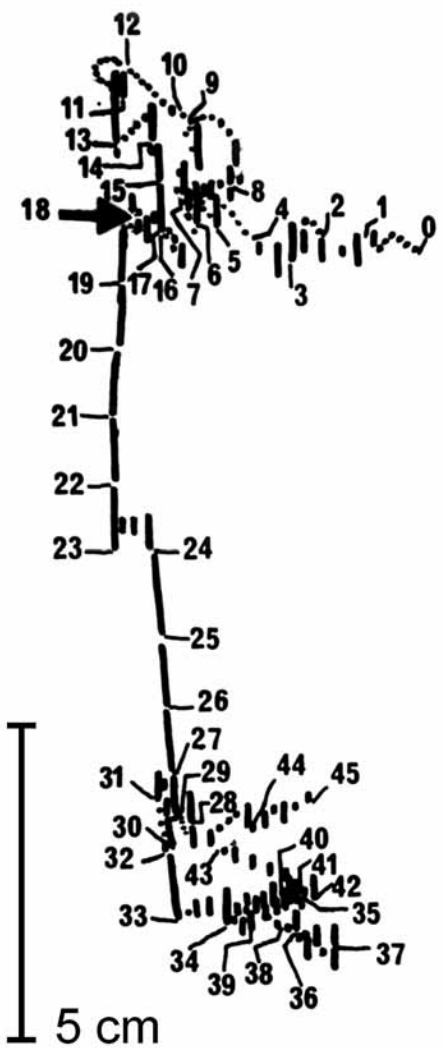

FIG. 6. – Motion pattern of *Cycloops abyssorum praealpinus* during 450 s. The animal swam with 50 others in a 5 L vessel at an irradiance of 0.5 erg cm^{-2} s^{-1} (Strickler, 1969). After 180 s the light level was decreased suddenly by 18%. the animal reacted by being motionless for 50 s and after a few hops (10 S) remained motionless for another 40 s. It then resumed normal swimming. (Data from Strickler, 1969).

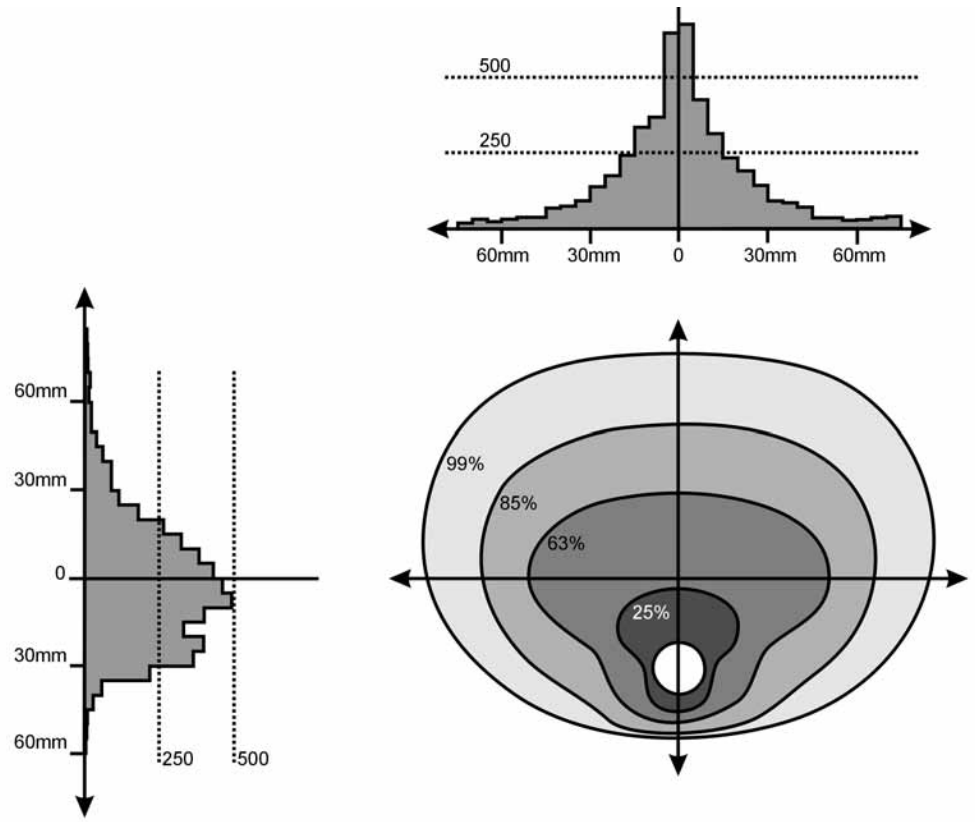

FIG. 7. – Distribution frequencies of *Cyclops abyssorum praealpinus* after 30 s while starting at the origin. All animals were swimming with a pattern as during the first 180 s in Fig. 6. 10% of all cases would be within the white circle because they were only sinking for the 30 s. Vertical and horizontal frequency distributions reflect this fact as well. (Redrawn from Strickler, 1969).

small volume, a cube of 50 mm edge length. After this time period a sudden change of light, a deduction of 18% at 0.5 erg cm^{-2} s^{-1} triggered an immediate stop of all motions; the animal began to sink, made one hop and continued to sink for a total of 30 seconds. Then it resumed swimming around at random as if no interruption has happened. Buskey and Hartline (2003) observed a similar behavior in a totally different copepod species in marine waters. We interpret this behavior with what the animal would do when suddenly fish show up and cause a change in the light intensity the zooplankter perceives. They in turn behave like dead particles—akinesis mimicry.

To test whether or not the animals swim in a random fashion Strickler (1969) changed the reference point of analysis along the swim tracks with the goal to note where the animal will be in 30 seconds with reference to the position it is now. This analysis is only performed during the first three minutes of observation before any changes of environmental conditions occurred. Figure 7 summarizes the results from 4730 such vectors. 10% of all vectors stem from sinking (inner white circle in Fig. 7). The general structure of the two-dimensional figure is a flattened onion-shell. It is flattened because the animals swim more pronounced in the horizontal direction than in the vertical one. The figure also shows the bias to sink rather than to swim down. If we analyze the frequency distributions we can see in the horizontal direction a somewhat over emphasized preference for staying around the origin, again due to the sinking bias, but also due to the two-dimensional nature of the representation of a three-dimensional phenomenon. In the vertical direction the sinking bias shows up clearly, but again one can see that a Gaussian distribution is underlying the details.

From these results we can conclude that swimming at random could be used as a reasonable assumption. Recent research using observation with the full three-dimensional resolution and more modern mathematical treatment will result in more detail about the swimming tracks of micro-crustacean zooplankton (e.g. Bundy *et al*., 1993; Doall *et al*., 1998; Seuront *et al*., 2003; Uttieri *et al*., 2004).

If planktivorous fish, especially small coral reef fish, prey upon planktonic copepods with success, then they have to perceive whatever little difference there is between a dead floating particle and a live copepod. They have to zero in on small differences

within short time similarly to chicken walking with other chicken over an area with randomly distributed seeds as their food. There is intense competition who can see it first and no wasting time picking the wrong item.

CAN FISH DISTINGUISH BETWEEN PARTICLES OF DIFFERENT MOTION PATTERNS?

Only limited research has examined predator selection based on prey swimming patterns, due mostly to the difficulties in the control of zooplankton swimming behavior. The use of computer-generated virtual prey offers a solution to this problem. Prete *et al*. (2001) studied the responses of male praying mantises to computer-generated visual stimuli. Using images either lacking or possessing certain attributes of the mantis' normal prey, they were able to determine which visual characteristics the mantis used to identify its prey. Brewer and Coughlin (1996) created virtual plankton (VP) that mimicked the size and swimming behaviors of actual plankton. This system allowed them complete control over the exact movements of their zooplankton prey, with which they examined bluegill preference for different speeds of randomly moving VP.

For our study we used the same basic equipment setup as Brewer and Coughlin (1996), with slight modifications, to investigate predator choice based on zooplankton swimming patterns. The virtual plankters are small black ovals displayed against a gray background. All virtual plankton are of realistic zooplankton size, measuring 1mm wide and 1.5 mm tall, displayed on a 640 x 480 pixels (35 x 27 cm) monitor (Panasonic Video Monitor Wv-5470) directly sealed to an aquarium (50 x 20 x 22 cm). The front end of the aquarium is curved so as to fit securely against the convex screen and adhered with transparent silicone caulk. A divider was placed in the aquarium 25.5 cm from the screen during trials to limit the volume of the testing arena. A camera (SONY near-infrared CCD video camera XC-EI50) is mounted 54 cm above the aquarium wall, opposite the monitor, to observe and videotape the selections of the fish. A large black cloth was used to cover the entire experimental set-up in order to eliminate outside distractions and prevent any positional bias by the fish due to light. The only light within the setup came from the monitor. A near-infrared light (Supercircuits infrared illuminator 15-IL05-USA), invisible to the bluegill (Protasov, 1970), was suspended 56 cm over the center of the aquarium to aid the videotaping of the experiment. Water temperature was monitored and no significant change was apparent due to the presence of the near-infrared light.

For all trials we used the Cararra Studio™ animation program to create virtual plankton. In Cararra Studio™ three-dimensional objects are created within the Assemble Room on a coordinate map. We adjusted the parameters in order to project a natural size of our Virtual Plankton. We then adjusted the speed of the animation to 30 frames per second and the length of the timeline sequence to 20 seconds.

In order to create animations in Carrara Studio™, we created "key frames" at points in time along the timeline. We reposition the objects throughout the space at each key frame along the desired motion path. After each key frame, we move the object to its new position in the next key frame. For our purposes the objects moved in a straight line from the position in one key frame to the next one in the next key frame. The objects also moved at a constant velocity between key frames. For our study, it was necessary for the VP to move to an exact position in a certain amount of time to ensure a specific velocity. At each key frame, we needed to enter the exact coordinates of the VP's new position. We devised a way to import coordinates directly from a Microsoft Excel™ spreadsheet into the Carrara Studio™ document.

We were able to use real data to reproduce the motion paths of actual *Daphnia*. Data provided by Nihongi (for methods see: Strickler, 1998; Nihongi *et al*., 2004) was generated from actual measurements taken of live *Daphnia pulex* swimming behaviors using Trackit (Iguana, v.2.0) to digitize the videos. This data allowed us to exactly mimic the timing and movement patterns of the *Daphnia*. The speed of the hopping VPs was determined to be 6.6 mm s^{-1} when displayed on the monitor. Nihongi also provided data for spinning *Daphnia* induced by fish kairomones. The speed of the spinning VPs was determined to be 18.1 mm s^{-1} when displayed on the monitor.

For our first experiment, we animated a pair of VP displayed 6 cm apart from each other in the center of the screen. One individual moved in the real hop and sink pattern, while the other was the real spinning VP. We varied the VPs according to which side (left or right) they started, at what point in the motion path they began, or in which direction (left or right) they moved, so that no two VPs were ever

paired together in the same way. We made fifteen movies, each 17.2 seconds long.

For our second experiment, we also presented the fish with a pair of VP beginning their movement in the same positions as the first experiment. One VP swam in a hop and sink pattern along the straight line. The second VP traveled in a smooth straight line without the hop and sink pattern. It required only two key frames to make the second VP, one at the origin and one at the final point. The final key frame located the VP at a distance equal to that of the final distance of the hopping VP. Consequently, both VP had the same net velocity. It also moved in a random direction determined by a TI-89 random number generator. We made 15 total animations, each 20 seconds long.

For our next experiment, we decided to use real data. We therefore took the data for hopping and spinning *Daphnia* and determined the average speeds of both. We determined a ratio of 18.1/6.6. Using this ratio, we extended the length of the animation in Carrara™ of the spinning VP to 47.2 seconds. This resulted in both VPs moving at the speed of 6.6 mm s^{-1}. As in the first experiment, the animation consisted of a pair of VP spaced 6 cm apart in the same positions. Again we varied the direction, position, and starting point of the motion path of the two VPs. Each animation was 17.2 seconds in length. For further definitions of VP patterns see Table 1.

Each animation was continuously looped to last the length of each trial period. This was done to prevent the VP from moving so far apart as to not be recognizable as a single pair or set by the fish. We rendered each animation at 30 frames per second in Carrara Studio™. We saved the video files as AVI files and imported them into Adobe Premiere™. From Premiere™, we exported the videos to a small monitor, where we monitored that the video had exported properly. Once we were sure the animation was running fine and our experiment could begin, we rerouted the video and displayed the animation on the aquarium monitor for the fish.

Bluegill times of response to VP varied from two seconds to over a minute, although we only recorded those trials that lasted under a minute. The bluegill would usually hover at the back of the testing arena and observe the VP for some time before making an approach and subsequent attack (Fig. 8). Often the bluegills exhibited a dorsal tilt before making a final approach towards the VP, although this was not always the case. Once the fish touched the TV monitor screen it received a live *Daphnia* as positive reinforcement. It did not matter where on the screen the contact was made, or which VP was the choice, in order not to introduce a bias.

In our first experiment, the bluegill chose the real spinning VP over the real hop and sink VP significantly more than would be expected by random choice ($\chi^2 = 18.46$, $p > 0.001$, $df = 1$). In our second experiment, bluegill showed no significant preference for either VP moving smoothly in a straight line or in hop and sink in a straight line ($\chi^2 = 0.75$, $p > 0.25$, $df = 1$). In both of these experiments, there was no significant left-right bias displayed by the fish ($\chi^2 = 0.08$, $p > 0.99$, $df = 3$). In our next experiment, we found that the while the bluegill still chose the spinning more than the hop and sink, there was no longer a significant difference from random choice ($\chi^2 = 2.17$, $p > 0.1$, $df = 1$). There was no significant left-right bias displayed by the fish during this experiment ($\chi^2 = 3.65$, $p > 0.05$, $df = 1$). The percentages for each of the individual fish were arcsin

TABLE 1. – Definitions of motion patterns of the virtual plankton (VP).

Observed Spinning	VP motion was created from data provided by Ai Nihongi of live *Daphnia pulex* swimming behavior. The speed of the VP is 18.1 mm s^{-1}.
Observed Hop and Sink	VP motion was created from data provided by Ai Nihongi of live *Daphnia pulex* swimming behavior. The speed of the VP is 6.6 mm s^{-1}.
Observed Slowed-down Spinning	Same data as Observed Spinning motion path, but the path was extended to 47.2 seconds, consequently, slowing the speed to 6.6 mm s^{-1}.
Linear	VP is moving linear in a randomized direction at a speed of 2.72 mm s^{-1}.
Simulated Hop and Sink	VP is traveling in a constant direction in which each successive hop is at 45° (or -45° depending on the initial direction) relative to the previous hop. Each hop is 1.27 mm and takes 0.2 sec. Each sink moves directly downward 0.36 mm and takes 0.04 sec. The VP moves at 2.72 mm s^{-1}.
Random Hop and Sink	The VP travels in a hop and sink motion in which each successive hop occurs at a randomly selected angle, between 45° and -45°, relative to the previous hop. The distance and time of each hop and each sink movement is the same as in the Simulated Hop and Sink. The VP moves at 2.72 mm s^{-1}.
Simulated Spinning	The VP follows a hop and sink motion in a spiraling path in which each successive hop is at 45° (or -45° depending on the direction of the spiral) relative to the previous hop. The distance and time of each hop and each sink movement is the same as in the Simulated Hop and Sink. The VP moves at 2.72 mm s^{-1}.

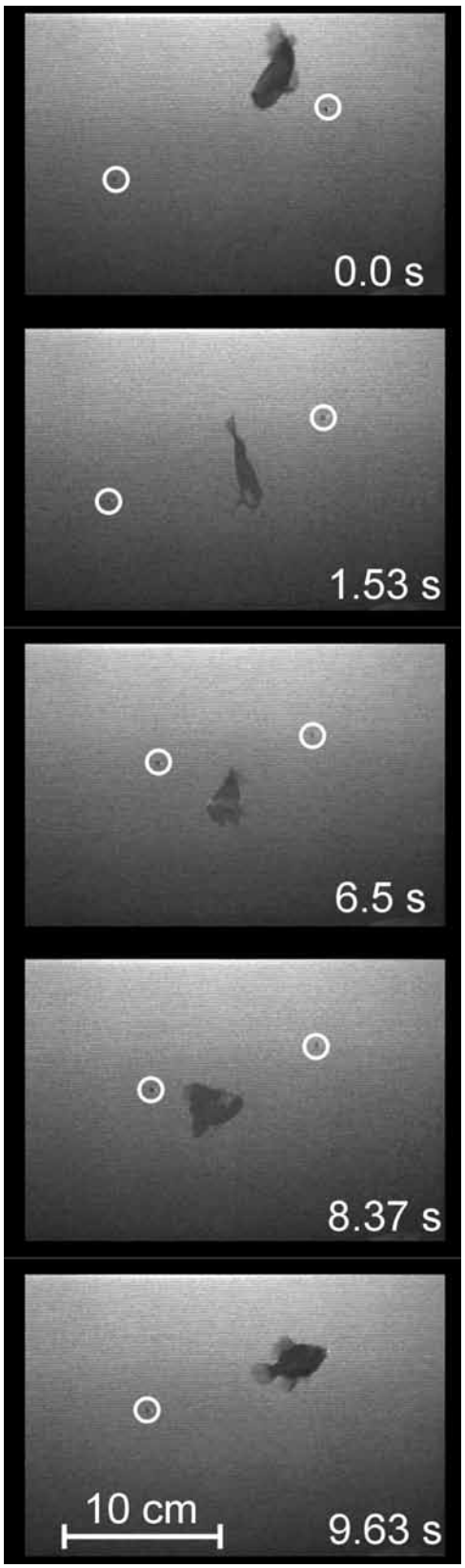

FIG. 8. – Frames from a video recording of *Lepomis macrochirus* selecting the virtual plankton on the right. At 0.0 s the fish swims closer to the left virtual plankton at 6.5 s before chanching orientation toward the right one at 8.37 s, and finally picking on the right virtual plankton at 9.63 s.

transformed and a one-way ANOVA revealed that there was no significant difference between the fishes' choices ($F_{3,16} = 0.911$, $P = 0.457$). This shows that the fish all had similar abilities and preferences when choosing the VP. Table 2 shows a complete list of results from our experiments.

HYPOTHESES

Our fish watched the two targets for a short time period (Fig. 8 is a typical sequence), compared the two moving VPs, and decided which one to attack. The visual environment was very dark and no other landmarks would have helped the fish to distinguish between the two VPs. We casually tested some of our colleagues and found that none could reach the accuracy of our fish. Therefore, we assume that these experiments with virtual targets suggest that our fish, and maybe most planktivorous fish, see their surrounding environment differently than we humans see our world.

Let us explain the difference: when we take a picture with a camera, for example with an exposure time of one millisecond, we can later recognize this picture; we can recognize what the picture represents. It could be a familiar face, or it could be a rainy landscape. Hearing for us is very different than vision. If we would hear just one millisecond of music we would not recognize the piece of music. We have to hear a few seconds of sound to guess what the name of the tune is. Contrarily, our fish had to observe the visual targets for a few seconds before attacking the preferred VP. In other words, the fish had to "listen" to the motions of both targets to select one.

The assumption then is that our fish see the way we humans hear; that the visual signal processing in the nervous system follows an algorithm similar to the one our hearing employs. Needless to state that much more research is necessary to justify this assumption. Since these experiments are the first ones cornering this question complex, we can—for this additional research—formulate the hypothesis that "planktivorous fish perceive the visual temporal pattern of suspended particles and chose targets on the basis of the motion pattern."

We can also formulate a second hypothesis when we include the fact that there are planktivorous fish not only on coral reefs but also within the open water column. The major difference between the two environments is the background. The blue water

TABLE 2. – Selection frequencies for each experiment. The numbers in bold represent how many times the fish selected the motion pattern in bold over the other one.

Fish	**Observed Spinning** vs. Observed Hop&Sink	**Observed Slowed-down Spinning** vs. Observed Hop&Sink	**Simulated Hop&Sink** vs. Linear	**Simulated Hop&Sink** vs. Random Hop&Sink	**Random Hop&Sink** vs. Simulated Spinning
1	**9**, n=15	**10**, n=15	**8**, n=15	**11**, n=15	**10**, n=15
2	**14**, n=15	**3**, n=6	**8**, n=11	**8**, n=15	**12**, n=15
3	**9**, n=15	**7**, n=15	**6**, n=14	**10**, n=15	**13**, n=15
4	**14**, n=14	**8**, n=10	**5**, n=8	**5**, n=10	**10**, n=12
Total	**46**, n=59	**28**, n=46	**27**, n=48	**34**, n=55	**45**, n=57
Ave.% ± SD	80 ± 21 %	61 ± 15 %	56 ± 12 %	62 ± 11 %	79 ± 9 %

one may be as uniform as a blank piece of paper, whereas the coral reef one is most likely highly complex. Therefore, the second hypothesis could be formulated as "planktivorous coral reef fish have the additional skill to analyze small moving particles in front of a complex background." The interesting question here would be: if the complexity of the motion pattern matches the complexity of the background, does the suspended particle vanish?

The counterhypothesis would be that fish go after the outstanding, most intriguing moving item, a notion we should not forget and may have some evidence for if we compare the two first columns of Table 2 where one motion pattern was slowed down and is now not so interesting anymore.

ZEBRAFISH TO THE RESCUE?

The predator-prey relationship we discussed above is a very dynamic one. The predators as well as the prey are suspended in water. Their global positions are constantly changing with the flow of their surrounding water. Additionally, the relative position of the prey in relation to the mouth of the fish is also changing; the more turbulent the water is the faster it changes. At the same time, many other suspended particles move about—again, the more turbulent the water is the more complex the situation. Within the blue water column of oceans and larger fresh-water bodies the fish does not perceive any fixed landmarks. Even the sun, a much larger fuzzy disk, is constantly moving due to the wave actions. This means that the fish cannot rely on measuring angles between a fixed point and the different suspended particles to figure out which ones behave differently from the others. How to recognize a food item, a live copepod for example, among all the other suspended particles is our topic here.

Many contributions have been published concerning the visual and other sensory systems of fish (e.g. Douglas and Djamgoz, 1990; von der Emde *et al.,* 2004). Certainly the structure of the fish's eye and the signal processing capabilities make it possible that planktivorous fish catch their food. One strategy has been mentioned by Kils (1989): swim in schools. Even if one fish attacks a copepod and this prey escapes, one of the next fishes will catch it because the copepods gets exhausted and cannot escape anymore with the same deployment of speed. However, our fish here does not school and still catches copepods.

Let us concentrate on eye structure and signal processing. As with all vertebrates, the fish retina is a stratiform structure composed of 3 cellular layers and two synaptic layers (Cajal, 1892), which together detect light, determine characteristics of the light information such as intensity, angle, velocity, wavelength, direction, and transmit the processed information to the brain where an image is perceived. The photoreceptor cells, which absorb the light, reside at the back of the retina transmit this information to interneurons in the inner nuclear layer, which process the information, and distribute it to the retinal ganglion cells, which transmit the information to the brain. The topography of the retina, how densely or sparsely the cells are distributed within the different layers, determines where in the visual field an object is perceived in the greatest detail. In primates, cone photoreceptors and ganglion cells are most densely packed in the central part of the retina in a highly specialized region called the fovea, where visual acuity, or detailed vision, is highest. Other vertebrates also have highly specialized regions of the retina where retinal neurons are more densely packed, however these specialized regions are not always centrally located as in mammals. Instead of the fovea, in many ani-

mals the specialized regions is arranged linearly in a structure referred to as the "horizontal streak". In fish the arrangement of these specialized regions correlates with both the anatomy and the ecology of the fish at any given stage its life history (Bozzano and Catalán, 2002; Collin and Pettigrew, 1989; Tamura and Wisby, 1963).

In this discussion we are concerned not only with spatial acuity, but also temporal acuity since we are considering whether fish use the motion pattern of copepods in distinguishing their prey from non-food particles. In fish, the retinal ganglion cells project to three different nuclei all of which could play a role in motion detection: the accessory optic area (AOS), the pretectal complex (PTC) and the tectum opticum (TO) (Maaswinkel and Li, 2003). Maaswinkel and Li (2003) argue that the TO is most likely to play this role given its involvement in escape and approach responses. In addition to visual input, motion detection is also likely to involve auditory inputs as well as mechanosensory inputs from the lateral line both of which have been shown to play roles in processing of water currents and in the larval escape response (Higgs and Fuiman, 1996; Montgomery *et al.,* 2000). It is possible that the summation of such inputs results in the superior abilities of the fish to accurately select and acquire its prey.

The aforementioned comparison of vision with hearing is only as good as to point out that the signal processing of the visual stimuli must accommodate the recognition of temporal patterns. Clearly the structures of the sensory systems of eyes are very different from that of ears. How then would we investigate the signal processing in planktivorous fish when it comes to recognizing temporal swimming patterns of copepods and other zooplankters? The question may find a solution in recent and future research on the sensory system of zebrafish.

One of the great strengths of zebrafish as a model system is the availability of a variety of genetic tools that can facilitate the discovery of molecular determinants of behavior. The rapid development and transparency of the zebrafish embryo, combined with the use of fluorescent transgenic reporter genes, allows the visualization of discrete populations of neurons throughout development (e.g. Udvadia *et al.,* 2001; reviewed in Udvadia and Linney, 2003). The ability to visualize such populations, in turn, allows us to selectively lesion or ablate such populations for functional analyses (reviewed in Gahtan and Baier, 2004). Forward genetic approaches are also powerful tools that allow the isolation of mutations that have specific effects on the structure and behavior of the developing retina (Gross et al., 2005; reviewed in Pujic and Malicki, 2004). How can such methodology forward our understanding of vision as it pertains to the predator-prey relationship? With the proper development of robust behavioral assays in zebrafish we have the potential to genetically dissect the various components of prey selection and acquisition, which will provide a starting point for assessing how the visual system functions in diverse feeding behaviors amongst teleosts.

In conclusion, we can state that the definition of visibility, which includes the many different components determining visibility, is reflected in the predator-prey relationship between plankivorous fish and their food, planktonic copepods. Our recent research and the discussion of its results show that we still wonder more than we can explain. However, adapting approaches from our colleagues investigating zebrafish we may find the answers faster than when going our own ways.

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