The behavior of Pacific herring schools in response to artificial humpback whale bubbles

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Abstract: There have been numerous reports of humpback whales and other marine predators deploying bubbles during foraging activities. However, the effects of bubbles on schooling prey organisms remain poorly understood. We conducted a series of laboratory experiments to gain insight into the effect of bubbles on the Pacific herring, *Clupea harengus pallasi*, a principal prey species of the humpback whale, *Megaptera novaeangliae*. The fish exhibited strong avoidance of bubbles and could be contained within a circular bubble net. The herring schools were also reluctant to swim through a curtain of bubbles even when frightened. However, herring were much more willing to cross a bubble curtain or net if there was a larger aggregation of fish on the opposite side. Individuals and small groups of herring also waited for less time before crossing than did larger groups. These experiments suggest that herring have a strong fear of bubbles and can readily be manipulated or contained within bubble nets by predators.

Résumé : De nombreux travaux signalent la production de bulles au cours des activités de recherche de nourriture chez les Rorquals à bosse et chez d'autres prédateurs marins. Cependant, les effets de ces bulles sur les bancs de proies sont encore mal compris. Nous avons procédé à une série d'expériences en laboratoire dans le but d'essayer de comprendre l'effet des bulles sur le Hareng du Pacifique (*Clupea harengus pallasi*), l'une des principales proies du Rorqual à bosse, *Megaptera novaeangliae*. Les harengs évitaient activement les bulles et ils pouvaient être contenus dans un réseau circulaire de bulles. Les bancs de harengs hésitaient également à traverser un rideau de bulles, même en cas d'alerte. Cependant, ils traversaient plus volontiers un tel rideau de bulles s'il y avait un banc relativement important de poissons de l'autre côté. Les individus et les petits groupes hésitaient moins longtemps que les grands groupes avant de traverser. Ces expériences indiquent que les harengs sont très apeurés en présence de bulles et ils peuvent être facilement maîtrisés par leurs prédateurs ou contenus à l'intérieur de réseaux de bulles.
[Traduit par la Rédaction]

Introduction

The release of bubbles during foraging activity has been noted in a number of marine predators, including the killer whale, *Orcinus orca* (Simila and Ugarte 1993), spotted dolphin, *Stenella frontalis* (Fertl and Würsig 1995), grey whale, *Eschrictius robustus* (V. Deecke, personal communication), fin whale, *Balaenoptera physalis* (S.S. Sadove, personal communication), Bryde's whale, *Balaenoptera edeni* (H. Wada, personal communication), river otter, *Lutra canadensis* (F.A. Sharpe, unpublished data), humpback whale, *Megaptera novaeangliae* (Ingebrigtsen 1929; Jurasz and Jurasz 1979; Hain et al. 1982; Baker 1985; D' Vincent et al. 1985; Baraff et al. 1991; Weinrich et al. 1992), and several species of alcids (Sharpe 1994). Compared with other predators, the humpback whale is unusual in that it deploys bubbles in a much more elaborate manner, and utilizes bubbles while foraging on a variety of prey species, including schooling fishes and euphausiids.

Humpback whales are known to produce a variety of bubble structures, often in conjunction with other unusual feeding behaviors such as the broadcasting of low-frequency sounds, group hunting, and flashing their very large pectoral flippers at prey (Brodie 1977; Baker 1985; D' Vincent et al. 1985; F.A. Sharpe, personal observation). Ingebrigtsen (1929) first documented the release of air by humpbacks when he noted the species capturing krill in circular bubble nets. Jurasz and Jurasz (1979) made extensive observations in southeast Alaska, where they described the use of bubble nets on both krill and schooling fishes. In the North Atlantic, Hain et al. (1982) described humpbacks utilizing a number of bubble structures including nets, curtains, and clouds. In addition, there are a number of reports of foraging techniques, including flick-feeding and lobtailing, where bubbles are injected into the water column by a rapid movement of the flukes (Jurasz and Jurasz 1979; Hain et al. 1982; Weinrich et al. 1992), which may also constitute a use of bubbles to manipulate prey organisms.

There has been considerable speculation as to how bubbles assist in capturing prey. Most observers have noted that predators use bubbles to frighten or herd prey, although whether it is the acoustic, visual, or mechanical characteristics of the bubbles or a combination of these attributes that elicit a response from fish is not known. Ingebrigtsen (1929) suggested that bubbles were visually detected by krill and used to frighten the crustaceans into the center of bubble nets. Jurasz and Jurasz (1979) noted that bubbles can be used to contain prey spatially and serve as a barrier against which to herd them. Hain et al. (1982) suggested that bubbles may aid in the detection of prey or serve to mask the approaching whale. Weinrich et al. (1992) speculated that the bubble cloud produced by a lobtailing whale may mark a spot of high prey

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concentration for the subsequent lunge. Experiments in the laboratory showed that herring could avoid a curtain of air bubbles in the dark, suggesting that the fish were not relying on vision to detect the air curtain (Blaxter and Batty 1985). In laboratory experiments, Akiyama et al. (1992) found that jack mackerel, *Trachurus japonicus*, also avoid bubble curtains during both light and dark conditions. In one of the few attempts to replicate humpback whale bubble structures in the laboratory, Kieckhefer (1991) found that small bubbles could disorient euphausiids and drive them to the surface. The effectiveness of bubbles in containing the movement of fish schools has also been demonstrated by their use in small-scale bait-fishing operations (Smith 1961). In this commercial application, a bubble curtain is used to trap fish within the upper portion of a fjord during high tide, permitting easier capture.

Although previous studies have been instructive, there have been no attempts to bring schooling fish into the laboratory to test their response to bubble structures similar to those produced by humpback whales. We conducted a series of laboratory experiments with the objective of gaining insight into the effect of bubbles on fish schooling activity. These experiments examined whether Pacific herring, *Clupea harengus pallasi*, could be physically contained within the boundaries of a bubble net, and if a herring school was willing to cross a bubble curtain when frightened by a predatory stimulus. We also conducted a third experiment when we found that the tendency of a herring school to cross appeared to be influenced by the relative numbers of fish on the two sides of the bubble curtain. In particular, we noted that small schools tended to escape from the bubble net more frequently than large schools. In our study, we tested the following predictions: (*i*) that a herring school will spend more time in the confines of a bubble net relative to an equivalent space in a control with no bubbles, (*ii*) that herring will avoid crossing a bubble net even when exposed to a predatory stimulus, and (*iii*) the larger the school on the opposite side of the net, the more frequently a school will cross through a bubble curtain and the less time it will wait before initiating a crossing.

Materials and methods

This study was conducted at the West Coast University Marine Biological Station (WCUMBS), Bamfield, B.C., during the spring of 1993 and 1994. Experiments were conducted indoors in a large (200 000 L) circular aquarium 2.8 m deep and 27 m in circumference. A smaller outdoor circular tank (1.7 m depth × 3.1 m circumference) was used for the group-size crossing experiments. Lighting for the indoor tank was provided by four 200-W flood lamps and from indirect light entering through a 1 × 0.6 m hole in the ceiling. Bubble structures were produced by turning a control valve that allowed 50 PSI compressed air through 5-cm PVC tubing perforated with 0.3-mm holes. The perforated PVC tubing was anchored to the tank floor by securing it to two additional PVC pipes packed with gravel. The bubble curtain produced in this way resembled those produced by humpback whales, in terms of both overall circumference and individual bubble diameter (Hain et al. 1982; personal observation).

The herring used in the experiments were captured live in Bamfield Inlet, Barkley Sound, on 2 June 1993 and 20 May 1994 with a 60-m hand seine. The fish were taken from a stock of prespawning 2-year-olds averaging 14 cm total length and 22 g body mass. Care was taken to minimize stress to the fish by quickly transferring them to the Station, where they were placed in a dark, outdoor circular (1.7 × 3.1 m) holding tank. Any fish exhibiting more than 15% scale loss or abnormal schooling behavior were removed from the experiment.

Experiment 1: Bubble-net crossing

The objective of this experiment was to test whether a herring school encircled by a bubble net would have its movements restricted compared with a control school without bubbles. In total, 18 trials were conducted, 10 during the spring of 1993 and 8 during the spring of 1994. The bubble net was produced by placing a 6.5 m diameter ring of perforated PVC tubing in the center of the aquarium floor, approximating the size of nets produced by humpback whales in the wild. The tubing was drilled with 22 holes spaced about 0.3 m apart. When the air valve was turned on, water was gradually displaced from the tube, the hole closest to the high-pressure line being the first to produce a bubble column. As water continued to be displaced from the tube, each of the holes produced a bubble column in clockwise succession, resulting in a circular bubble curtain (comprised of coalescing columns) that took approximately 7 s to fully close. Each bubble column was composed of a dense, cone-shaped air jet with individual bubbles ranging in diameter from a few millimetres to 15 cm. A breakwater constructed of transparent plastic was floated in the center of tank, producing a smooth pool of water (5.5 m diameter) that permitted videotaping through the surface turbulence created by the bubbles. Fish behavior was recorded with a video camera located 4 m above the water's surface. Analysis of the videotape was conducted with a VHS freeze-frame player.

On the evening prior to each experiment, a school of 50 fish was placed in the large tank and permitted to acclimate overnight. The bubble treatment commenced the following morning by videotaping the school of 50 fish when it made a crossing through the center of the tank. If 25 or more members of the school crossed inside the ring of PVC tubing, the air valve was turned on. If at least one individual was trapped within the confines of the bubble net, the air remained on until all the fish escaped. If no fish escaped, the air was turned off after 60 s. If the entire school escaped the bubble net before it closed, the air was immediately turned off and a 5-min waiting period ensued prior to the next trial. A similar procedure was conducted for the controls, except that the air was not turned on. Each of 18 schools received both the control and the bubble treatment, in random order. The crossing durations (i.e., the time required for 50% of the school to cross from the inside of the PVC ring to the outside) in the control and treatment trials were then compared with a Wilcoxon's signed-rank test. Crossing frequencies were compared for schools of different sizes (Kruskal–Wallis test).

Experiment 2: Fright stimulus and crossing tendency

The purpose of this experiment was to determine whether a herring school could be induced to swim through a curtain of bubbles if frightened. The experimental apparatus consisted of a perforated PVC pipe laid down along the center line of the large aquarium. The pipe was drilled with 26 holes spaced 34 cm apart. A floating breakwater was placed above the PVC pipe, providing an undisturbed section of water on one side of the curtain for videotaping. The procedure for acclimating the fish and recording their behavior was the same as in exp. 1.

Each treatment began when the bubble curtain was turned on to trap the school on one side of aquarium (chosen at random). The bubble curtain remained on for 60 s, during which time the school was exposed to a fright stimulus consisting of 5 thrusts with a plunge pole (a 15 cm diameter rubber plunger on the end of a 3-m PVC pole). Thrusts to a depth of 1.5 m were delivered at 10-s intervals from a stationary point and directed toward the school. Crossings were tallied each time an individual fish, or the entire school, crossed the tank center line in either direction. A school was

Table 1. Initial capture and retention success of the artificial bubble net (exp. 1).

Trial No.	No. caught (of 50)	Proportion caught	No. escaped	Proportion retained	$T_{treatment}$ (s)	$T_{control}$ (s)
1	17	0.34	1	0.94	60	3
2	20	0.40	20	0.0	28	6
3	25	0.50	0	1.0	60	7
4	31	0.62	0	1.0	60	2
5	32	0.64	5	0.84	60	4
6	35	0.70	0	1.0	60	4
7	38	0.76	17	0.55	60	3
8	50	1.0	0	1.0	60	8
9	50	1.0	0	1.0	60	5
10	50	1.0	0	1.0	60	6
11	36	0.72	4	0.89	60	2
12	28	0.56	3	0.90	60	3
13	50	1.0	0	1.0	60	4
14	16	0.32	16	0.0	14	1
15	50	1.0	0	1.0	60	7
16	22	0.44	22	0.0	9	2
17	10	0.2	4	0.4	60	3
18	26	0.52	0	1.0	60	1
$\bar{x}$					52.8	3.9
SD					16.8	2.1

Note: The proportion caught is the proportion of the herring from the school of 50 individuals that were initially trapped inside the bubble net. The proportion retained is the proportion of the school remaining in the bubble net after 60 s. $T_{treatment}$ is the time during which the bubble net remained on. (Note that if the entire school escaped, the bubbles were turned off before the 60-s trial time had elapsed.). $T_{control}$ is the time required for 50% of the fish to leave the equivalent space when no bubbles were present.

considered to have crossed when 50% or more of the individuals swam over the center line. The same procedure was conducted during the controls, with the exception that the bubble curtain was turned off. In total, 10 schools were tested, each of the schools receiving both the control and the experimental treatment. The numbers of crossings in the controls and treatments were then compared using a paired *t* test.

Experiment 3: Crossing tendency and group size

The purpose of this experiment was to examine the effect of group size on the tendency to cross. This was done by varying the number of fish on each side of a bubble curtain to determine if a smaller group exhibited a greater tendency to cross to the larger school. This experiment was conducted in the outdoor circular tank fitted with a perforated PVC pipe down the center line. The pipe was drilled with 11 holes placed 15 cm apart. Each trial utilized a group of 8 fish that was permitted to acclimate to the tank for a minimum of 3 h prior to testing.

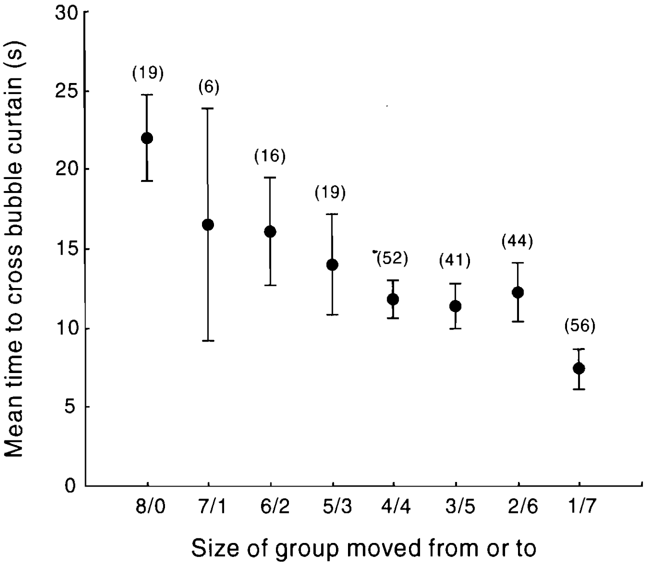
The experimental procedure involved varying the number of fish on each side of the bubble curtain so that all five possible combinations of group sizes were tested (8/0, 7/1, 6/2, 5/3, and 4/4) for each school of fish. To minimize any bias in crossing due to the features of the tank, each combination of fish was tested twice, with the numbers on the two sides of the bubble curtain reversed (i.e., 8/0, 0/8, 7/1, 1/7, etc.). This resulted in a total of 10 crossing tests for each batch of fish. The order in which the 10 combinations of group sizes were tested was randomized. At the start of each trial, the fish were split into two appropriately sized groups by turning on the bubble curtain as the school passed over the center line. The time elapsed until the first fish crossed through the bubble curtain (from either direction) was recorded. If there were no crossings, the air was shut off after 60 s. A 5-min waiting period was implemented before the next trial was conducted. This process was continued until all 10 combinations had been tested. A total of 32 different batches of fish were tested in this fashion. The waiting times prior to crossing for the different group sizes were then compared using Kruskal–Wallis and χ^2 tests.

Results

Experiment 1: Bubble-net crossing

Fish schools encircled by the bubble net spent a mean of 52.8 s in the center of the tank, while controls spent a mean of 3.9 s there (Table 1). Fish were significantly more likely to remain in the center portion of the tank when encircled by a bubble curtain (Wilcoxon's signed-rank test, $P < 0.0002$). This clearly indicates that a circular curtain of bubbles can spatially contain the movement of a herring school. We compared the frequencies of outward crossings (escapes) for trials with 1–24, 25–40, and 41–50 herring initially captured in the bubble net. Crossing frequencies differed significantly between these three groups (Kruskal–Wallis test, $P = 0.0048$). Indeed, on the five occasions when the entire school was captured in the bubble net, no escape crossings occurred. However, when smaller groups were captured in the net, the proportion of individuals escaping during the 60-s trial was much higher (means of 73.2 and 12.8% for group sizes 1–24 and 25–40, respectively). And on several occasions, small groups of fish were observed to swim into the bubble net (through the closing gap) in order to join a larger group of herring on the inside.

Fig. 1. The mean time required for an individual herring to cross the bubble net plotted against the size of its school relative to that on the other side of the net (exp. 3). For example, if there were initially seven fish on one side and one on the other, an average of 16.5 s was required for one of the fish from the school to cross the net, though this happened infrequently (n = 6); much more often (n = 56) and more quickly (mean 7.4 s), the lone individual crossed to join the group. Every group-size combination was tested 64 times, twice for each of 32 herring schools. Numbers in parentheses are sample sizes.



Experiment 2: Fright stimulus and crossing tendency

A mean of 5.8 individual fish (SD = 12.9) crossed the bubble curtain during the treatments (Table 2). In contrast, the mean number of individual crossings for the no-bubble controls was 178.6 (SD = 48.6). Fish were significantly less likely to cross the center line of the tank (paired t test, $P < 0.0001$) when the air curtain was on. Similarly, whole school crossing events were significantly less common (paired t test; $P < 0.0001$) during the bubble treatments ($\bar{x}$ = 0.1, SD = 0.31) than for the no-bubble controls ($\bar{x}$ = 3.3, SD = 3.3; Table 2).

Experiment 3: Crossing tendency and school size

As was the case in exp. 1, there was a correlation between group size and crossing tendency, with smaller groups more frequently swimming across the bubble curtain to join the larger group (Table 3). For example, in the 1/7 group trials, the solitary individual initiated the crossing in 88% of the trials. In the 8/0 group trials, the school exhibited a strong tendency to remain on one side of the tank, with no crossing occurring in 70% of the trials. Smaller groups also waited less time before crossing (Fig. 1; Kruskal–Wallis test, $P < 0.0001$).

Discussion

Taken as a whole, these experiments reveal that herring take strong evasive action in the presence of a curtain of bubbles and are reluctant to swim through it, even when frightened. Bubble nets are capable of spatially containing an aggregation of herring, even in a region of the tank they normally avoid (i.e., the center). The tendency of individuals to cross a bubble curtain is strongly mediated by relative group size, with individuals or small groups of fish more likely to cross if there is a larger group on the other side. In addition, individuals and small groups wait less time before crossing than larger groups. This study also showed that a herring school would swim into a closing bubble net if there was a larger group of fish on the inside.

Table 2. The influence of bubbles on the tendency of herring to cross the center line of a large aquarium (exp. 2).

	N	$\bar{x}$	SD	P (two-tailed)
No. of individual fish crossings				
Bubbles	10	5.8	12.9	
No bubbles	10	178.6	48.6	<0.0001
No. of whole-school crossings				
Bubbles	10	0.1	0.31	
No bubbles	10	3.3	0.82	<0.0001

These findings confirm field observations that humpback whales use bubbles to manipulate prey behavior by constraining the movement of fish schools. The strong avoidance responses of herring noted in the laboratory suggest that whales may use bubbles to herd fish into more exploitable spatial arrangements (such as tight aggregations) or force the school upward in the water column, thus trapping them against the surface.

That fish will cross through a bubble curtain to join a larger group (minority departure rule) has previously been reported (without any supporting data) by Radakov (1973), and is analogous to the findings of other studies. For example, Hager and Helfman (1991) found that in the presence of predators, minnows chose larger shoal sizes, made their choices more quickly, and exhibited a heightened ability to discriminate shoal size. Itazawa et al. (1978) noted that fish in smaller groups are more nervous and have higher respiratory rates. In the wild, herring schools are known to fluctuate widely in size over a 24-h period (Carson 1984; Robinson 1991). Consequently, the size of the school may be an important factor in determining how fish respond to an enclosing bubble net deployed by humpbacks. The observation of fish entering a closing bubble net in this study suggests that a bubble net may have a capture area greater than its actual diameter, if fish outside the net are enticed into it by a larger group on the inside.

Given the general reluctance of herring to cross bubble curtains, it was rather puzzling to find in exp. 3 that fish in the 0/8 and 8/0 trials crossed fairly regularly to the side with no fish. Schools of 8 waited a relatively long time to cross ($\bar{x}$ = 22.0 s); perhaps they became somewhat habituated to bubbles and therefore more willing to do so. In addition, it was frequently a single fish that crossed over after becoming separated from the main school. The increased vulnerability of a solitary individual to predators (see below) may favor actions that increase the likelihood of a lone fish promptly relocating school mates.

Most studies that have examined interactions between predators and fish schools have used predators that focus their attacks on solitary individuals. These studies have demonstrated that individuals separated from a group are more likely to be captured by a predator (Magurran and Pitcher 1987; Godin and Smith 1988; Parrish et al. 1989) and that the predation

Table 3. The influence of relative group size on the willingness and speed with which herring cross a bubble curtain (exp. 3).

Group-size combination	Crossings to larger group[a] No.	Crossings to larger group[a] Time (s)	Crossings to smaller group No.	Crossings to smaller group Time (s)	No. of trials without crossings[b]	P^c
0/8, 8/0	—	—	19	22.0	45	
1/7, 7/1	56 (88)	7.4	6	16.5	2	<0.001
2/6, 6/2	44 (69)	12.3	16	16.1	4	<0.001
3/5, 5/3	41 (64)	11.4	19	14.0	4	<0.001
4/4, 4/4[d]	52 (81)	11.8	—	—	12	

[a]The number of times that an individual crossed from the smaller to the larger group, and the mean time required to do so. The numbers in parentheses are percentages of crossings (out of 64) from the side of the net with fewer fish to the side with more fish.

[b]The number of occasions (out of a total of 64 trials on 32 schools) in which no crossings occurred.

[c]From a χ^2 test of the hypothesis that the direction of first crossing is independent of the relative numbers of fish on the two sides of the bubble curtain.

[d]With a group-size combination of 4/4, there is, of course, no larger or smaller group.

success of aquatic piscivores decreases when prey group size increases (Neill and Cullen 1974; Milinski 1979; Tremblay and FitzGerald 1979; Poole and Dunstone 1975). Such feeders (fish, seabirds, and pinnipeds) may be the dominant predator type encountered by herring and other bait fishes; thus, their best strategy will usually be to close ranks whenever they are threatened. It is interesting to note, however, that these schooling behaviors appear to be less effective, or even detrimental, in response to bulk-feeding predators such as baleen whales. When the air was first turned on during each of the trials in this study, any fish located near or above the rising bubble plumes reacted with a strong flight response directly away from the bubbles. In the wild, fish may perceive rising bubbles as the approach of a predator, and thus execute an inappropriate response to the bulk-feeding humpbacks below.

Whether it is the acoustic, mechanical, or visual characteristics of rising bubbles that are most frightening to herring and other schooling fishes is not known. It is likely, however, that the effectiveness of these three stimuli varies under different environmental conditions. As a fish swims it generates a wake of counter-rotating vortices (Pitcher and Parrish 1993). School mates appear able to detect these vortices using otoliths and lateral-line organs up to one fish length away, and can use them to synchronize schooling activities (Gray and Denton 1991). The strong mechanical disturbance created by rising bubbles (Fan and Tsuchiya 1990) may be disruptive to the school's flow regime, making effective avoidance maneuvers more difficult. This appears similar to Strand and Hamner's (1990) finding that krill, *Euphausia superba*, were reluctant to school in turbulent water, apparently because of the confusing rheotactic (mis)information compared with the normal turbulence produced when swimming. In one of the few other attempts to replicate humpback whale bubble structures in the laboratory, Kieckhefer (1991) found that small bubbles could disorient euphausiids and even drive them to the surface, owing to microbubbles trapped underneath their carapace or adhering to their feeding appendages.

Our experiment provided some evidence that herring may also be responding to the acoustic and visual components of rising bubbles. When the bubble net or curtain was first turned on, fish up to several metres away (well beyond the range of mechanical influence of the bubbles) would respond with pronounced startle or avoidance maneuvers. Playbacks of bubble sounds were found to produce a moderate avoidance response from herring, further suggesting that the acoustic component of a bubble structure may be used to manipulate fish behavior by humpbacks in the wild (F.A. Sharpe, unpublished data). Observations of humpbacks deploying bubble nets at night (L. Dawson, personal communication) further implicate acoustic or mechanical influences. However, the possibility that herring are responding to the visual component of bubbles at night cannot be ruled out, as bioluminescent organisms may make bubble nets highly visible. Further field investigations are required to better understand how varying environmental conditions influence the manner in which fish schools respond to bubbles. However, this study provides strong evidence that the deployment of air can be a highly effective tool for humpback whales and other predators of schooling fishes.

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