# FISHY TALES: BEHAVIOUR OF SCHOOLING FISH ESCAPING FROM TERNS

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## ABSTRACT

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The aim of this study is to develop a better understanding of seabird foraging behaviour and the anti-predator behaviour of their prey. Studies of seabirds' foraging and prey-capture behaviour, as it relates to the evasive and escape behaviour of schooling fish, are sparse. Our study was carried out at One Tree Reef on the southern end of the Great Barrier Reef, Australia. A school of hardyheads *Pranesus capricornensis* sheltered in the shallows over the sand flats in front of the research station for 14 non-consecutive days. In that time, Lesser Crested Terns *Thalasseus bengalensis* were observed for 10 hours from above the surface in 37 foraging bouts and for 40 minutes from underwater in at least one foraging bout. In each foraging bout, a single tern dived into the school. We found that terns on average dived at a rate of 0.67 ± 0.35 dives/minute from 4–5 m above the surface. The depth range of dives was 43–58 cm. Therefore, fish within 58 cm of the surface were potentially accessible. The total length of the hardyheads was 10–12 cm, which is within the size range useable by terns. Fish used flash expansion to escape diving terns and formed a vacuole around birds as they slowly ascended to the surface. This escape manoeuvre was effective about 80% of the time. The fish that were caught did not respond to the escape movements of the fish above them and, therefore, were isolated. Fish also used the C-startle response to escape terns underwater and in mid-air. The anti-predator manoeuvres of hardyheads are similar to those observed among *Clupea* spp. (herrings and sardines) and *Ammodytes* spp. (sand eels) escaping sub-surface predators. Hardyheads and sardines react in the same way to gannets *Morus* spp. and terns that plunge dive directly to their prey, partially confirming the prediction that results for plunge-diving gannets are generalisable to other gannets and boobies (*Sula* spp.), terns and gulls (*Larus* spp.), tropicbirds (*Phaethon* spp.), pelicans (*Pelecanus* spp.), and kingfishers (Alcedinidae).

**Key words:** foraging behaviour, predatory behaviour, confusion effect, atherinids, silversides, mathematical model

## INTRODUCTION

The foraging behaviour of seabirds has been studied intensively but lacks observations on the evasive and escape behaviour of their prey. How can we understand the foraging behaviour of seabirds, what they do, and why they do it, when we do not understand how their prey react to them (see Crook & Davoren 2014)?

We effectively have two disparate branches of literature: one focused on seabird foraging and the other focused on reactions of schooling fish to sub-surface predators. For example, the seabird literature has concentrated on indirect observations of foraging behaviour (e.g., biologging) of pursuit divers such as penguins (Spheniscidae; Wilson *et al.* 1996, Tremblay & Cherel 2000), alcids (Alcidae; Burger & Simpson 1986, Burger *et al.* 1993, Mehlum *et al.* 2001, Elliott *et al.* 2008, Shoji *et al.* 2015), shearwaters (Procellariidae; Burger 2001, Peck & Congdon 2006), cormorants (Phalacrocoracidae; Wilson & Wilson 1988, Gómez-Laich *et al.* 2012), as well as plunge divers such as gannets (Sulidae; Nelson 1978, Ropert-Coudert *et al.* 2004) and terns (Laridae; Dunn 1973, Erwin 1977, Duffy 1983, Safina *et al.* 1988, Hulsman 1989). None of these studies have examined the evasive and escape behaviour of their prey for good reason: few researchers have had the opportunity to view the interaction between the birds and their prey from underwater.

Recent advances in technology have brought together the behaviour of the predator and the reactions of their prey. Researchers can now video fish evading and escaping from marine predators, including seabirds. Footage has been obtained by free divers filming the predator-prey interaction (e.g., Machovsky-Capuska *et al.* 2011) and by mini-cameras attached to the bodies of penguins (e.g., Gómez-Laich *et al.* 2018). Despite these innovations, the focus has remained on the birds' behaviour and not the behaviour of their prey. Two notable exceptions are Axelsen *et al.* (2001), who used multibeam sonar to record the escape behaviour of herring *Clupea harengus* from pursuit-diving Atlantic Puffins *Fratercula arctica*, and Crook & Davoren (2014), who used fixed cameras to reveal the predator behaviour of pursuit-diving Common Murres *Uria aalge* and the anti-predator behaviour of capelin *Mallotus villosus*.

Most studies of seabirds underwater lack details about the evasive and escape manoeuvres of fish schools when seabirds attack them. For that information, it is necessary to consult fish biologists. They have studied the evasive manoeuvres of fish in the laboratory (reviewed by Domenici 2010), in computer simulations (e.g., Podila & Zhu 2017), and in the field (e.g., Axelsen *et al.* 2001). Briefly, there are three phases of predator behaviour: (1) predator *detects* prey; (2) predator *chases* prey; and (3) predator *attacks* prey. For the prey, the correlates of these three phases are: (1) prey *detects* predator; (2) prey *avoids* predator; and (3) prey *escapes* predator. Fish schools use at least seven detection/avoidance manoeuvres in the predator's first two phases (detect and chase) and five escape manoeuvres in the third phase (attack; see Podila & Zhu 2017). The correlating predator/anti-predator behaviours are paired as follows: detect-detect (herd, inspection, vacuole), chase-avoid (avoid, cruise, compact, skitter), attack-escape (ball, flash expansion, fountain, hourglass, split; see Pitcher & Wyche 1983, Magurran & Pitcher 1987).

Some seabirds rely on sub-surface predators like tuna (Hulsman 1979) and dolphins (Vaughn *et al.* 2008, 2010), which circle the school while foraging, packing it into a ball and herding it to the surface, where seabirds and other predators can access them (Hulsman 1979; Vaughn *et al.* 2008, 2010). Many species benefit from this behaviour and thus schools of fish are often attacked by Multispecies Feeding Associations (MSFAs) involving seabirds (gannets, terns, shearwaters, alcids; Au & Pitman 1986, Camphuysen & Webb 1999), predatory fish (sharks and tuna; Hulsman 1979, Au & Pitman 1986, Clua & Grosvalet 2001), and marine mammals (seals, dolphins, whales; Duffy 1983, Au & Pitman 1986, Hodges & Woehler 1994, Vaughn *et al.* 2008, Gómez-Laich *et al.* 2012, Thiebault *et al.* 2016). MSFAs attack prey from many directions in quick succession, fragmenting the school and making it easier for birds, smaller predatory fish, and mammals to catch solitary fish (Götmark *et al.* 1986, Thiebault *et al.* 2016). Thus, capture rates increase and all predators benefit (Thiebault *et al.* 2016).

Evasive manoeuvres used by schooling fish tend to be similar for all sub-surface predators, but their escape manoeuvres depend on the predator's hunting method. A predator approaching a school usually elicits an increase in the swimming speed of the school, which also compacts by decreasing the distance among nearest neighbours (Litvak 1993, Podila & Zhu 2017). Attacks directed at the periphery of the school elicit "flash expansion"—the fish in the predator's path scatter simultaneously in all directions except towards the predator (Partridge 1982). However, if a predator enters the school at speed, it may elicit "split"—the school forms separate groups—or it may elicit a "fountain manoeuvre", in which the school splits into two, passes on either side of the predator, and regroups behind it (Partridge 1982, Pitcher & Wyche 1983, Podila & Zhu 2017), and eventually return to the main body of the school if possible. On the other hand, if a predator swims slowly into a school, the fish will "inspect"—they create a vacuole (a space around the predator) and then observe its behaviour at a safe distance for any change in its intention (see Magurran & Pitcher 1987, Pavlov & Kasumyan 2000).

Schools of fish respond with the same variety of escape manoeuvres to pursuit divers (e.g., puffins), which, like predatory fish, can attack a school from any direction, for several seconds, and repeatedly, especially if there is a group of them (Axelsen *et al.* 2001). In this paper, we fill an important gap in the literature by integrating the predatory behaviour of plunge-diving birds with the anti-predator behaviour of their fish prey. We relate what we observed in the field to what has been described in the literature and filmed by other researchers to show the generalisability of patterns to other plunge-diving birds and schools of fish. We developed a simple mathematical model using key variables to explain the spatial and temporal details of how a schooling fish, the hardyhead *Pranesus capricornensis*, escapes from Lesser Crested Terns *Thalasseus bengalensis* plunge diving into their midst.

## STUDY AREA AND METHODS

The study area was at One Tree Reef (23°27′S, 152°05′E) in the Capricorn Group, Southern Great Barrier Reef. During low tide, Lesser Crested Terns hunted schools of hardyheads (atherinids; 10–12 cm total length) when they sheltered in the shallows of the sand flats on the reef in front of the research station. The school was stationary, 3–4 m long, 2 m wide, 0.4–0.5 m deep, and contained a few thousand fish. The school's location facilitated the collection of data on foraging terns above and below the water during low tide. One Tree Reef is shaped like a saucer or a large tidepool; during the spring tides, there is no water exchange between the ocean and the lagoon from three hours after high tide until three hours before the next high tide. Thus, the water level did not change during our observations.

We used mixed methods (quantitative and qualitative) to record the dynamics of the interactions between diving terns and their prey. The qualitative data, which are descriptions of how the fish reacted to the terns, were the same for the 14 dives observed underwater and the 362 dives observed from above the water, all less than 6 m from the school.

Above-water observations involved recording the heights and angles from which terns dived, the number of dives, and the number of fish caught. There were 13 observation periods consisting of 37 foraging bouts during which one tern was observed from above the water diving into a school of hardyheads. The 13 observation periods lasted about 10 hours in total; the shortest period of observation was about 9 min and the longest more than 156 min (Table 1).

Underwater observations involved a diver wearing SCUBA gear observing terns as they dived into a school for approximately 40 minutes consisting of at least one foraging bout. The water was clear, and visibility was at least 6 m. The diver entered the water 15 m from the school, swam slowly towards it, and stopped about 3 m from it, so that the school did not move but could still be clearly viewed. The diver rested on the sand substrate at a depth of 63 cm and minimised their movements. Observations were recorded on grey plastic sheets in pencil.

**TABLE 1**
**Summary of data of Lesser Crested Terns *Thalasseus bengalensis* foraging on hardyhead schools, as observed from above water**

| Observation | No. foraging bouts | Duration (min sec) | No. dives | No. fish caught | Foraging success (%) |
|---|---|---|---|---|---|
| 1 | 1 | 38′ 20″ | 22 | 2 | 9.1 |
| 2 | 1 | 34′ 20″ | 11 | 4 | 36.4 |
| 3 | 3 | 66′ 20″ | 47 | 9 | 19.1 |
| 4 | 4 | 70′ 35″ | 53 | 10 | 18.9 |
| 5 | 6 | 156′ 05″ | 60 | 21 | 35.0 |
| 6 | 1 | 17′ 50″ | 7 | 1 | 14.3 |
| 7 | 1 | 37′ 50″ | 13 | 7 | 53.8 |
| 8 | 4 | 54′ 45″ | 40 | 2 | 5.0 |
| 9 | 1 | 22′ 10″ | 28 | 6 | 21.4 |
| 10 | 2 | 55′ 50″ | 7 | 2 | 28.6 |
| 11 | 6 | 19′ 08″ | 20 | 2 | 10.0 |
| 12 | 6 | 21′ 27″ | 31 | 5 | 16.1 |
| 13 | 1 | 9′ 10″ | 23 | 1 | 4.3 |
| **Total** | 37 | 603′ 50″ | 362 | 72 | |
| | | **Mean** | 27.8 | 5.5 | 20.9 |
| | | **Standard deviation** | 17.5 | 5.5 | 14.3 |

The depth to which a tern dived was measured at the tip of its bill against where, on a coral head behind the school, the tern stopped. Parallax error was minimised by the diver changing their depth to be in line with the tern, which stopped long enough at the maximum depth of the dive for the diver to adjust position. However, to avoid disturbing the school repeatedly to measure the dive depth, only the minimum and maximum dive depths during an observation period were measured, using a 30 m spooled measuring tape. The depth was measured in two stages: from the substrate to the fixed point on the coral head and from substrate to the surface. The end of the tape was anchored on the substrate under the diver's heel and the other end was held in line with the surface. Thus, the maximum depth could be measured (± 0.5 cm). The minimum depth was also measured in two stages, from the substrate to the spot where the tern had reached and then to the surface. The accuracy of this measurement was ± 4 cm.

## RESULTS

Lesser Crested Terns plunged perpendicular to the water surface into the middle of the school at a mean rate of 0.67 dives/min (standard deviation (SD) = 0.35 dives/min, $n$ = 13 observation periods). The attacks were quick, lasting < 0.2 s. Terns dived from heights of 4–5 m. Their mean foraging success was 20.9% (SD = 14.3%, $n$ = 13).

From above the water, the fish did not overtly respond to swooping terns. In contrast, the fish responded to a diving tern with flash expansion, creating a vacuole around the submerged bird (Fig. 1). The school surrounded the submerged tern and did not regroup until the tern had returned to the surface. This same response was observed for each of the 362 dives.

Underwater, a more detailed picture emerged. The minimum depth reached was 43 cm, the maximum was 58 cm, and the tern stopped within a few centimetres of the substrate. The terns relied solely on their momentum to reach their prey. Deceleration occurred very quickly: the bird was travelling fast then stopped suddenly, but the mechanism of deceleration is unclear. Between dives, the school was stationary, and all the fish were oriented in the same direction, towards the deeper water.

The underwater observations of the school's reactions to the diving terns were consistent with the above-water observations. Fish in the uppermost tier of the school reacted to the tern, but those below reacted to the fish above them (Fig. 1). Viewed from the side, the fish could not increase their depth sufficiently to escape from the diving tern because the water was uniformly shallow in the study area. The escape routes were therefore limited to the horizontal plane.

The evasive manoeuvres of the fish were well coordinated. Fish in the upper tiers of the school began moving just as, or immediately after, the tern broke the surface. The direction that the fish swam depended on their position relative to the tern's trajectory. Those in front of the tern's trajectory swam straight ahead. Those behind it turned 180° and swam out of the capture zone (Fig. 1). Those to the side of the tern's pathway turned less than 180° before swimming out of the capture zone. This effect spread like a wave vertically and instantaneously to the lower tiers of the school. The fish escaping from the capture zone slid between their neighbours, decreasing the distance between nearest neighbours. Viewed from above, the dispersing fish left a vacuole around the tern (Hulsman 1977, Partridge 1982; Fig. 1), and the school expanded in the horizontal plane. The fish surrounded the tern, oriented such that they could see the bird as it passively and slowly ascended to the surface. They remained stationary and regrouped below the tern

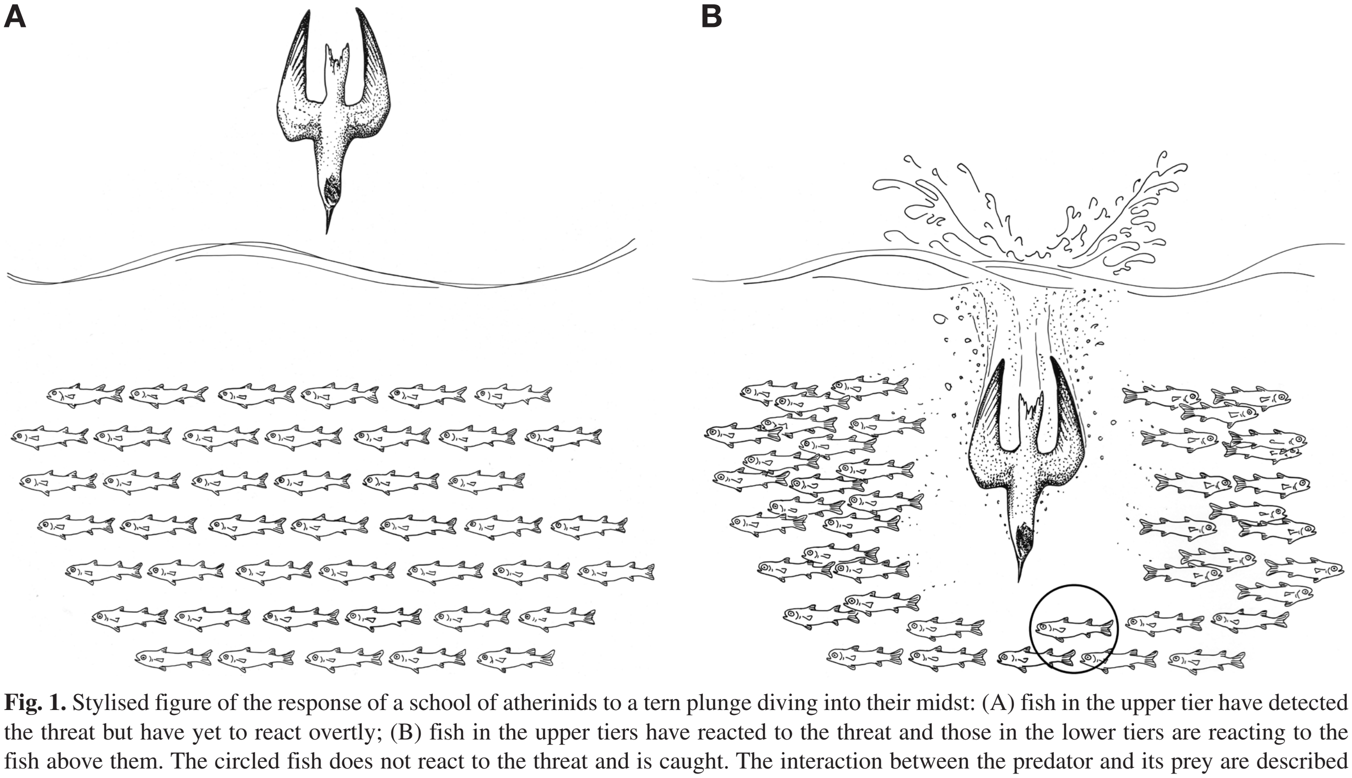

**Fig. 1.** Stylised figure of the response of a school of atherinids to a tern plunge diving into their midst: (A) fish in the upper tier have detected the threat but have yet to react overtly; (B) fish in the upper tiers have reacted to the threat and those in the lower tiers are reacting to the fish above them. The circled fish does not react to the threat and is caught. The interaction between the predator and its prey are described by Equations (2) to (7).

once it was at the surface. There was ample time to see how the fish responded in those hundredths of a second after the tern broke the surface. Once the fish regrouped, they re-aligned and all faced in the same direction.

Each of the three fish whose capture was observed underwater was among the lower tiers of the school. Even though they were in the tern's pathway, none of them reacted quickly enough to the evasive movements of the fish above them, and therefore were caught. The tern grasped the prey just behind the head near the opercula. Terns did not manipulate their prey underwater; that was done in mid-air. Most fish that were caught were observed in the air to be grasped near the opercula. Sometimes, fish were seized around the mid-riff or the tail. Upon resuming flight, terns tossed these fish into the air and re-caught them around the opercula if returning to the colony. Otherwise, a tern tossed the fish and re-caught it with its length aligned with the bird's gullet before swallowing it.

Some fish escaped in this mid-air phase using the C-startle response, a reflexive response in which a fish contracts its body into a tight C shape in one direction then the other to evade or propel itself away from danger. For example, a fish held by the tail bent its body then flicked itself free of the tern's grip (see Litvak 1993, Domenici 2010) and fell back into the water (4.2%, $n = 72$). Another fish escaped when tossed into the air (1.4%, $n = 72$): the fish bent its body and flicked itself straight, changing its trajectory, and the tern missed re-catching it. Nevertheless, most fish when caught, stayed caught.

**TABLE 2**
**Terms used in the Sine Model and their definitions**

| Term | Definition |
|---|---|
| $\alpha_i$ | Angle at which bird enters water (degrees from vertical) |
| $d$ | Distance bird travels underwater (m) |
| $d_B$ | Depth to which bird dives (m) |
| $d_F$ | Minimum distance fish swims to escape from bird (m) |
| $M_w$ | Mass of bird in saltwater (kg) |
| $T_D$ | Time required for bird to travel the distance to fish once detected (s) |
| $T_F$ | Time required fish to escape from bird (s) |
| $T_i$ | Time that $V_w > 0$ (s) |
| $T_L$ | Time required for fish to swim out of bird's range, i.e. one fish length (s) |
| $T_R$ | Reaction time of fish (s) |
| $T_\theta$ | Time required to bend its body in C-startle response to travel at any angle 0–180° (s) |
| $V_a$ | Velocity of bird on impact with the water (m/s) |
| $V_F$ | Velocity of fish when escaping from bird (m/s) |
| $V_w$ | Velocity of bird underwater (m/s) |
| $W_{ti}$ | Deceleration owing to water resistance at the ith time (m/s) |

## The Sine Model

To understand the details of the temporal and spatial dynamics in the interactions between terns and their prey, we developed a simple mathematical model; please refer to Table 2 for term definitions.

The depth to which a tern dives is affected by not only the height from which it dives but also its mass and the angle at which it enters the water. Consider the following simplified set of conditions, as a demonstration of why the angle of penetration affects the depth of a dive: let a tern obtain a specific velocity and momentum (mass × velocity) at the time it enters the water. Let us assume that gravity and the bird's buoyancy have negligible effects on the tern's path underwater, and that the deceleration owing to water resistance is the same, regardless of the angle of penetration or depth achieved. Thus, a tern will travel a distance of $d$ metres underwater, regardless of the angle of entry. But the depth ($d_B$) to which a tern travels is a function of the angle of entry ($\alpha_i$) and the distance travelled (Fig. 2). The relationship is given by:

$$d_B = d \sin \alpha_i \tag{1}$$

However, all dives into the school were perpendicular. If a bird makes no swimming movements, its underwater velocity $V_w$ at any time is a function of its initial momentum upon entering the water, its deceleration owing to water resistance, and the amount of time elapsed since entering the water. This is represented as:

$$V_w = M_w V_a - \frac{W_{ti}}{V_w} \tag{2}$$

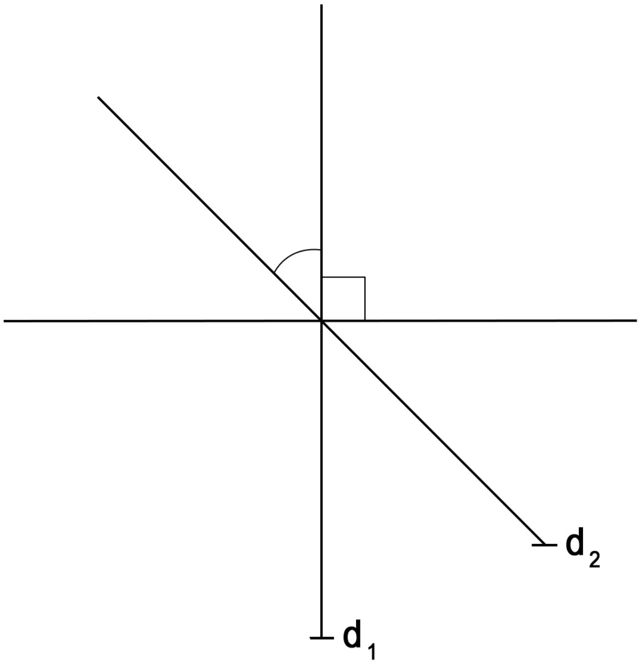

**Fig. 2.** The bird travels the same distance $d$ underwater, regardless of the angle at which it enters the water, $\alpha_1$. The depth reached depends on the angle of entry, all other things being equal. Depths $d_1$ and $d_2$ are the distances travelled when a bird enters the water at right angles and at angles less than 90 degrees, respectively. This is described by Equation (1).

The distance that a bird travels underwater $d$ is a function of its momentum ($M_w \cdot V_w$) and the amount of time ($T_i$) that its velocity $V_w > 0$. Therefore,

$$d_B = V_w T_i \tag{3}$$

and the distance that a fish swims $d_F$ is a function of its mean velocity $V_F > 0$ and time $T_F$. Thus,

$$d_F = V_F T_F \tag{4}$$

Therefore, the time it took a fish to swim out of a tern's reach is given by

$$T_F = \frac{d_F}{V_F} \tag{5}$$

The total time taken for a fish to move out of a bird's range $T_F$ is a function of its reaction time ($T_R$), the time to turn an angle of 0–180° ($T_\theta$), and the time it takes to swim the distance of its total length ($T_L$):

$$T_F = T_R + T_\theta + T_L \tag{6}$$

Thus, a fish is caught when $T_D < T_F$, or when it is within distance $d_B$ of the surface and when the time it takes to move out of the bird's range ($T_F$) is longer than the time it takes for the bird to close the distance from which it was detected by the fish ($T_D$). From equation (6) we get

$$T_D < (T_R + T_\theta + T_L) \tag{7}$$

By substituting values based on observations and literature into equation (7), the depth to which fish are accessible to diving birds can be calculated. Reaction times of golden shiners *Notemigonus crysoleucas* in a school varied between early responders (80 ± 30 ms) and late responders (255 ± 190 ms) in evading an aerial predator (Marras & Domenici 2013). These times can be used in the model as approximations for reaction times of hardyheads.

A tern may be submerged for 2–3 s, but most of that time is taken by the ascent to the surface. The time to reach their prey was < 0.2 s. For example, a tern travelling at 5 $\mathrm{m \cdot s^{-1}}$ would take 0.116 s to reach a depth of 58 cm and, therefore, a fish swimming at 5 $\mathrm{m \cdot s^{-1}}$ needed < 0.116 s (0.080 s reaction time + 0.036 s to escape) to escape. It would thus need to detect the tern at a distance of at least 58 cm, i.e., as the tern broke the surface. On the other hand, if a fish needed 0.140 s (0.100 s reaction time + 0.040 s to escape) to avoid capture, it would have to detect the tern at a distance of 70 cm, i.e., before it broke the surface. In response to each dive, the fish started swimming after the tern broke the surface. However, to evade capture, the fish in the upper tiers of the school would have had to detect the tern before it broke the surface. Any fish that had a reaction time of 0.255 s or more would have been caught; the tern would have reached the fish before it started to respond overtly.

## DISCUSSION

This simple model clarifies our understanding of the temporal and spatial dynamics of predator-prey interactions. In this case, examining how terns plunge dive direct to prey shows how they can catch prey more than a tern's length below the surface. Terns do not swim underwater but rely solely on the momentum that they attain in the dive. Their dive is an all-or-nothing attack lasting < 0.2 s. Therefore, they have more limited opportunities to catch prey than do gannets, which can change to a pursuit dive at the end of their plunge dive (see Ropert-Coudert *et al.* 2004).

A pursuit diver can attack from any angle, for longer duration, and with shorter intervals between attacks than can a plunge diver; the latter cannot catch prey from below. Consequently, effective evasive manoeuvres displayed by schools reacting to terns were limited to flash expansion and vacuole, whereas schools evading predatory fish and pursuit-diving birds used a wider range of evasive manoeuvres, e.g., fountain manoeuvre, flash expansion (see Partridge 1982), hourglass, split, vacuole (Pitcher & Wyche 1983, Axelsen *et al.* 2001). However, many pursuit divers snipe at the margins of the school and elicit flash expansion, catching any prey that are slow to respond or have been isolated from the school. In contrast, the plunge-dive attacks we observed came from above the school, were of short duration, and often targeted the densest part of the school. Fish needed to swim only a short distance to escape the aerial predator in its descent, and fleeing fish slipped between those outside the capture zone, decreasing the distance between neighbours. Thus, the school was compressed in the vertical plane but lengthened in the horizontal one, accentuating the confusion effect (see Litvak 1993). (The confusion effect happens when a predator's neural mapping of the position of the targeted prey becomes inaccurate when faced with multiple prey packed close together; Ioannou *et al.* 2008). The escape response created a vacuole and the fish remained out of bird's range while the bird ascended passively and slowly to the surface. The school regrouped when the tern was at the surface, after the threat had passed.

The maximum depth to which a tern can dive depends on the length of time that its momentum is greater than zero and the angle at which it enters the water (Fig. 2). Therefore, any fish in its pathway and within the depth to which it dives is potentially accessible. However, the depth at which a tern can catch any potentially accessible fish depends on the time it takes the tern to reach the fish once detected being less than the time it takes for that fish to evade it (Fig. 3).

The confusion effect probably contributed to the low foraging success of the terns. The diving rate was too low to disorganise the school for very long, and the fish had ample time to regroup before the next attack. Terns could not see the fish that they caught in the lower tiers of the school until the fish in the upper tiers moved out of the tern's path (Fig. 1). Similarly, fish in the lower tiers did not see the tern but responded to the movement of the fish above them. Fish in the upper tiers were moving out of the tern's path when the bird was between 10 and 20 cm from them, distances the tern would travel between 0.02 and 0.04 s, respectively. To escape, fish had to detect the bird at distances of 50–70 cm. Therefore, fish in the upper tiers of the school (< 20 cm from the surface) detected the tern before it broke the surface. To evade the tern, fish had to swim out of the capture zone before the tern arrived. This they could do if their reaction time was short (Fig. 3). In contrast, none of the three fish observed to be captured attempted to escape. They simply did not react to the sudden movement of fish above them, indicating that they had slow reaction times (Fig. 3). Was the low diving rate a result of the confusion effect created by the school? This requires further investigation.

Where a fish was seized by the tern would depend on how late it reacted to the tern. The later a fish reacted to a diving tern, the closer it would be grasped to the opercula. An earlier reaction would result in the fish being seized by the mid-riff; an even earlier reaction would result in the fish being seized by the tail. Observations from above the water revealed that most terns held fish around the opercula when they surfaced, which gives the tern the greatest control over the fish. Occasionally, the tern surfaced grasping the mid-riff or the tail; these fish were tossed in mid-flight and generally re-caught behind the head. Fish use the C-startle response to escape predators, with the amount of bend affecting the angle at which they swim away from the predator (see Domenici 2010). We observed some fish using the C-startle response to escape from terns in mid-flight. It was most effective when a fish was held by the tail because of the extra leverage from the body weight being to one side. When tossed into the air, one fish used this manoeuvre and changed its trajectory enough that the tern did not re-catch it, allowing it to escape. Thus, the amount of control a tern exerts over a fish depends on how far behind the head it is held, and the bird has greater control when holding the fish close behind the head.

Laboratory studies (see Partridge 1982, Litvak 1993) provide an accurate picture of evasive techniques used by fish (herd, cruise, spacing change in a plane oriented 90° to the direction of the attack). Simulations provide an accurate picture of escape manoeuvres used by fish reacting to sub-surface attacks (see Vabø & Nøttestad 1997, Podila & Zhu 2017; *cf.* Pitcher & Wyche 1983, Nøttestad & Axelsen 1999, Axelsen *et al.* 2001). There are two effective ways for schools of fish to escape from aerial predators plunge diving into their midst: to dive deeper out of their range or to execute a flash expansion followed by a vacuole. (Flash expansion is an escape response to a localised attack; a plunge dive is a localised attack.)

The observations in this study are representative of terns diving into deeper water because they submerged to > 60% of their estimated maximum diving depth. Furthermore, the plunge of the terns into water just over 60 cm deep was similar to the plunge of Cape Gannets *Morus capensis* into schools of sardines in much deeper water, but at a smaller scale.

The evasive reactions of fish are similar between three different families: Atherinidae (hardyheads; Partridge 1982); Clupeidae (sardines (BBC Earth 2014) and herring (Axelsen *et al.* 2001)); and Ammodytidae (sand eels; Pitcher & Wyche 1983). There are only so many ways that a school of fish can evade a predator, so responses of one schooling species are generalisable to others. Thus, we expect that capelin (Osmeridae), anchovies (Engraulidae), and juvenile tuna (Scombridae) would show the same evasive and escape manoeuvres as Atherinidae, Clupeidae, and Ammodytidae. Furthermore, the manoeuvres used by hardyheads escaping terns, which dive directly to their prey, are the same as those of sardines escaping gannets, which dive in a V-shaped trajectory (BBC Earth 2014 at the 0:11 mark of the video). Therefore, this partially confirms the Machovsky-Capsula *et al.* (2011) prediction that the reactions of fish to plunge-diving gannets are generalisable to other plunger divers, such as tropicbirds *Phaethon* spp., pelicans *Pelecanus* spp., kingfishers (Alcedinidae), and terns and gulls (Laridae).

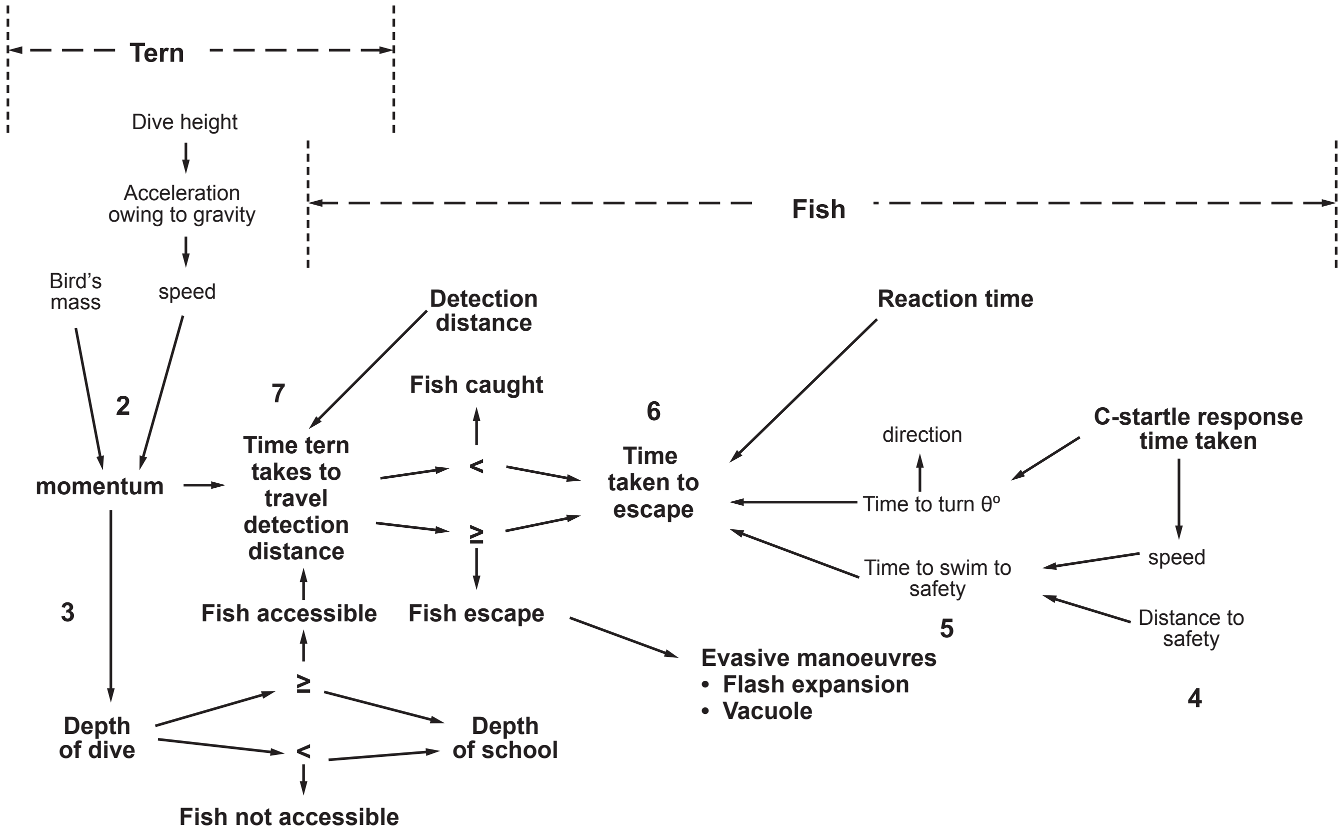

**Fig. 3.** Diagram of the model describing the interaction between a tern and a school of fish. The numbers refer to the equation provided in the text to describe that part of the process.

In conclusion, the results of our study confirm that the evasive manoeuvres of schools are similar for a variety of fish species. Field studies of species from three different fish families show that they use the same suite of manoeuvres to evade and escape from predators. The school expands at right angles to the direction of the attack (length and width), which increases the zone of confusion for a predator (Litvak 1993). The low frequency of terns attacking from above did not fragment the school. Therefore, terns were limited to catching fish that did not respond or responded too slowly to the threat. Consequently, the tern's foraging success in our study was low. Fish that escaped swam in the nearest direction not blocked by the tern's trajectory. The video footage of sardines (BBC Earth 2014) showed that the reactions of schools to plunge diving sulids are the same as hardyhead reactions to plunge diving larids (this study). We expect that the reactions of the fish are more widely generalisable to other plunge-diving birds such as tropicbirds, pelicans, kingfishers, gulls, and other terns.

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