Chapter 11
Immobility Behaviors in Fish: A Comparison with Other Vertebrates

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Abstract There are multiple types of immobility behaviors in the defense cascade in fish. Each immobility behavior has different functions depending on the imminence of the threat. The three major types include immobility during the orienting response, freezing, and tonic immobility (TI). The orienting response is elicited upon detection of any salient stimulus where the animal shows attentive immobility to maximize the monitoring of the environment and assess the seriousness of the situation. Freezing immobility is to minimize the possibility of detection by a predator. However, freezing is not merely a passive state but a continuous monitoring of the environment to seek a chance for escape. These two types of immobility behavior in fish share basic manifestations and biological similarities with those in land vertebrates. Only a limited number of reports show that TI in fish is functional in actual threatening situations, suggesting that TI is not a general defensive behavior in fish. Nevertheless, lines of evidence support the idea that the contribution of reflexive components in TI induction is conserved among vertebrates. Artificially induced TI is practically useful for safely manipulating sharks in the field. In some fish species, immobility-like behavior is used for feigning death or illness as a predatory tactic, instead of defensive behavior, to attract prey fish.

Keywords Death feigning · Defense cascade · Fish; freezing · Immobility behavior · Orienting response · Tonic immobility · Vertebrates

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11.1 Introduction

Immobility behaviors occur when animals face attentional and/or emotional situations that usually involve a predation risk. Animals stop ongoing behaviors to evaluate the situation or stimuli that are potentially significant for their survival. This is the first step of the defense cascade called the orienting response (Fig. 11.1). If the situation is found out to be threatening, the cascade proceeds to the next step: either fleeing or freezing. Then, if there is a further increase in the imminence of the threat and escape is not an option, animals fight back or show tonic immobility (TI). Various states of the defense cascade in mammals are briefly described in Chap. 1 of this book by exemplifying the case of a rat encountering a cat.

Thus, there are multiple types of immobility responses in the defense cascade, and each type has a different function depending on the context or the seriousness of the threat. In contrast to somewhat straightforward and explicable functions of orienting and freezing immobility, the biological significance of TI is not that clear, especially in fish, although it apparently often occurs in the terminal phase of antipredator behaviors.

In this chapter, I briefly overview the characteristics of three types of immobility behaviors, orienting, freezing, and TI, in vertebrates, mainly mammals, as components comprising a cascade of defensive behavior. For each type of immobility behavior, attempts are made to present examples in fish. Although a considerable amount of work on fish in this field has been published, the comparative biology of immobility behaviors in fish has not been thoroughly discussed.

11.2 Orienting Immobility

11.2.1 General Orienting Response in Vertebrates

The first step of the defense cascade is the orienting response that accompanies the immobility state. This step is activated upon detection of unfamiliar signs such as any disquieting sounds, vibrations, or odors. The cessation of ongoing or background stimuli can also be a salient sensory input to elicit an orienting response. If the novel or salient stimulus turns out to be of no significance, the orienting response wanes as the stimulus is repeated. This waning is not due to sensory adaptation but habituation of the response itself. Habituation is considered to be one basic type of learning (Petrinovich 1973). During orienting, the animal stops ongoing activity and reduces motion, which is referred to as “attentive immobility” (Volchan et al. 2017). An animal exhibiting the orienting response maximizes the monitoring of the environment by attentive immobility in which the posture is stabilized and muscle tone is increased (Kozlowska et al. 2015).

The orienting response is subdivided into two components: non-directional arousal, and directional attention towards the source of the arousing stimulus (Barry

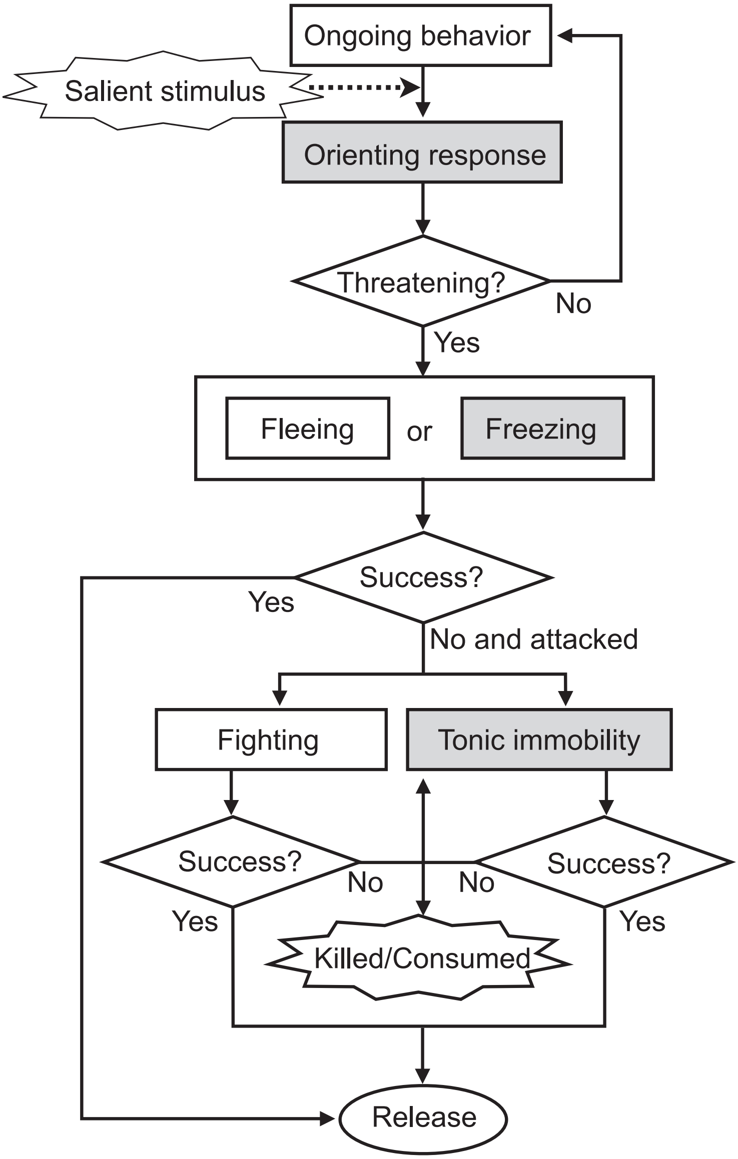

Fig. 11.1 A schematic representation of the defense cascade. Shaded behaviors include immobility states. See also Fig. 3.1 of Chap. 3

1984; Nicol and Laming 1993). During arousal, increased sensitivity of the sense organs is observed (Lynn 1966; Laming 1989). In humans, auditory sensitivity is enhanced by a preceding visual stimulus (Thompson et al. 1958) and vice versa (Watkins and Feehrer 1965). Increased sensitivity to a stimulus or facilitation of sensory neural activities during arousal has also been shown in other vertebrates, including fish (Laming 1989; Laming and Bullock 1991). Thus, the arousal state in the orienting response facilitates all sensory modalities to spot the source of the arousing stimulus.

In addition to sensory facilitation, physiological changes accompanying behavioral arousal include alterations in cardiac and respiratory activities. Heart rate and respiration rate decrease in the orienting response, especially during arousal, in various mammal species, including humans, dogs, sheep, and cats (Lynn 1966). The second state in the orienting response, attention, is aimed at the spotted source of the arousing stimulus.

Orienting should be comprehended integratively with motivation followed by appetitive or defensive emotional responses (Bradley 2009). This response is a part of the assessment process to examine a salient stimulus or a circumstance potentially related to positive (appetitive) or negative (fear or anxiety) emotions. Thus, the orienting response is not only for eliciting the defensive behavior but also for promoting an appetitive behavior, especially in predatory animals.

Immobility in the orienting response can also reduce the possibility of being noticed by a predator or by pray. As mentioned in Chap. 1 of this book, if the arousing stimulus is assessed as being originated from a threatening source, or predator, the next step of the defense cascade, flight or freeze, will take place.

Immobility during the orienting response shares some common features with freezing as a fright response: in both states, reduced motion and raised attentiveness are the characteristics. However, it should be noted that the substantial difference is that orienting immobility is a state of maximizing information gathering, while freezing is primarily a defensive/concealing reaction with heightened attention: the posture in orienting is usually upright or accompanied by small postural adjustments for redirection, while in freezing the animal commonly shows a tense crouching posture. Nevertheless, in many cases it is difficult to divide these two states clearly since the fright response can occur immediately upon the detection of a threat or if the novel stimulus is sufficiently intense (Lynn 1966; Laming and Savage 1980; Roelofs 2017).

11.2.2 Orienting Response in Fish

In fish, during the orienting response, there is an increase in muscle tonus, which is apparent from erected dorsal, abdominal, and anal fins, and an expanded tail fin (Fig. 11.2). Periodical twitching or continuous undulation of the pectoral fins is common, stabilizing the body in the water column. A decrease in heart rate and ventilation is also observed during the orienting response (Laming and Savage

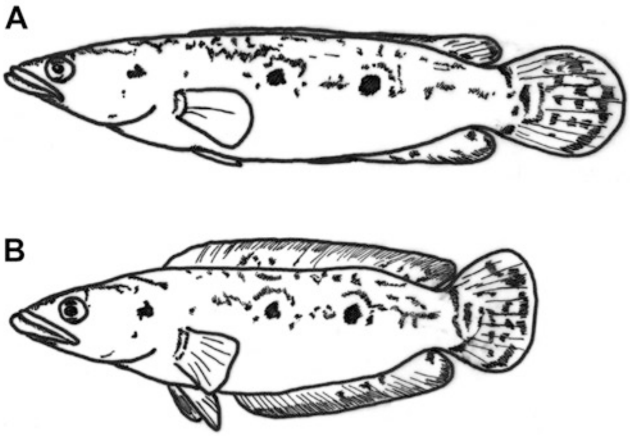

Fig. 11.2 Orienting response of the snakehead *Channa pleurophthalma*. (**a**) Resting posture. (**b**) A typical orienting response showing erected dorsal, abdominal, and anal fins, and expanded tail fin. Viewed from slightly diagonally from the front

1980; Rooney and Laming 1986). Fish shows quick habituation to an arousing stimulus when the stimulus is presented repeatedly (Laming and Savage 1980; Nicol and Laming 1993; Yoshida et al. 2004).

Attention, the latter phase of the orienting response, has been suggested to have the reverse physiological effect: increased heart rate (Laming and Bullock 1991) and attenuated sensory activity (Laming and Brooks 1985; Laming and Bullock 1991; Nicol and Laming 1993). It can be said, as in mammals, that during non-directional arousal, general facilitation of the sensory system and cardiorespiratory deceleration occurs, and in directional attention, selective inhibition of sensory input and cardiorespiratory acceleration takes place (Laming 1989).

The orienting response is apparently not obvious in some fish species. For example, although zebrafish have been widely used for studying flight (erratic swimming) or fright (freezing) responses, they do not show apparent behavioral arousal and attentive immobility as observed in some other fishes such as goldfish. A recent preliminary paper considers an approaching behavior towards novel visual stimuli as an orienting response (do Nascimento et al. 2019). In this case, however, the abrupt cessation of ongoing activity as in behavioral arousal and following attentive immobility, which are two major components of the orienting response, was not reported. Immobility as a part of the orienting response in fish could be a characteristic of species that show stable hovering in the water column.

11.3 Freezing Immobility

Following the initial risk assessment in the orienting response when the animal detects cues of an actual threat such as a predator, if not spotted, the animal exhibits the next stage of the defensive cascade in a species-specific way. If the threatening source is perceived as relatively distal, the animal at this stage has two alternative choices for a fear response, fleeing or freezing. Attentive freezing immobility is a common adaptive behavior to avoid detection by a predator (Whishaw and Dringenberg 1991; Eilam 2005; Chap. 1 in this book).

11.3.1 General Features of Freezing in Vertebrates

Immobility during freezing behavior is not merely a defenseless/motionless state, but rather an active preparatory stage with heightened alertness that facilitates sensitivity for the encounter of the threat (Eilam 2005; Gladwin et al. 2016; Rösler and Gamer 2019). In regard to the enhanced sensitivity and serving as an action-preparation state rather than a passive motionless state, attentive freezing immobility shares features with the orienting response (Gladwin et al. 2016; Roelofs 2017). Thus, freezing can also be a continuum of orienting-related immobility (Gabrielsen et al. 1985). Internally, fear elicited by the detection of threatening stimuli during the orienting response or by perceiving a learned cue related to an aversive situation seems to underlie attentive freezing immobility (LeDoux 2000).

Many factors including the anxiety level (Frank et al. 2006), context of the threatening situation (Eilam 2005; Blanchard et al. 2011), distance from the threat (Blanchard et al. 2011), and availability of escape routes (Blanchard et al. 1990) affect the decision of the dichotomy to flee or freeze (Eilam 2005; Hagenaars et al. 2014). Individuality or personality within species, either predisposed or experience-dependent, is also a factor contributing to the variety of fear responses (Gabrielsen et al. 1985; Budaev 1997; Eilam et al. 1999; Huntingford and Giles 2010).

The word "freezing" has been used to refer to a wide range of defensive immobility behaviors and is interchangeably used to describe different kinds of immobility responses to a threatening condition (Volchan et al. 2017; Chap. 1 in this book). Unlike other immobility states including TI, freezing is activated at an intermediate level of a threat to avoid detection by a predator. However, the anxiety context also elicits freezing. Although lines of evidence indicate a distinction between fear and anxiety, the behavioral manifestation of these emotional states might share some features including freezing in regard to the seriousness of a defensive situation.

Parasympathetic dominance, in addition to the systemic increase in muscle tonus, seems to be a major characteristic during freezing, causing cardiac deceleration in various vertebrates including humans. However, since freezing consists of both sympathetic and parasympathetic features, physiological changes vary depending on which system is dominant in the context even in the same species. In the case of classical conditioned fear, conditioned cardiac responses in similar classical fear conditioning paradigms differ in direction depending on both the animal species and condition (LeDoux 2000); restrained rabbits and rats (Kapp et al. 1979; Supple and Leaton 1990a) show bradycardia, whereas unrestrained rat (LeDoux et al. 1983; Supple and Leaton 1990b) and baboons (Smith et al. 1979) show tachycardia.

11.3.2 Freezing in Fish

Freezing immobility is also common in fish although studies specifically focusing on this behavior are not abundantly available compared to those for land vertebrates.

Since the finding of the "schreckstoff" by von Frisch (1938), alarm-substance-elicited fright reactions in ostariophysian fishes have attracted much attention (refer to Pfeiffer (1977) for a classical review; Brown et al. 2011). Along with fleeing and gathering, freezing is a major component of the fright reaction when exposed to an alarm substance released from the injured skin of conspecifics.

Freezing immobility in fishes is also commonly observed as a defensive behavior in prey fish visually exposed to a predator; ex. Nile tilapia *Oreochromis niloticus* (Cichlidae) (Barreto et al. 2003), darters *Etheostoma flabellare* and *E. spectabile* (Percidae) (Radabaugh 1989), three-spined stickleback *Gasterosteus aculeatus* (Gasterosteidae) (Messler et al. 2007), guppy *Poecilia reticulata* (Poeciliidae) (Templeton and Shriner 2004), and zebrafish *Danio rerio* (Cyprinidae) (Bass and Gerlai 2008).

With or without preceding orienting behavior, on detecting an imminent threat, a fish shows either apparently disoriented rapid swimming (erratic movement) or freezing immobility. These two fear-related behaviors frequently alternate multiple times: erratic movement followed by freezing and vice versa.

It seems that there are two types of freezing immobility in fish: one manifests when facing a threat and the situation shows the possibility of escape, and the other occurs when the success of escape is unlikely. Exposure to an alarm substance or a novel situation corresponds to the former case. Freezing in such cases accompanies cardiac and ventilatory accelerations (Laming and Savage 1980; Holopainen et al. 1997; Barreto et al. 2003). This is apparently in preparation for, or recovery from, erratic movement or rapid escape from the threat where intense motor activity is demanded. On the other hand, restrained fish have been reported to show cardiac and ventilatory decelerations as in classical conditioned fear responses (Davis and Holmes 1971; Yoshida et al. 2004).

Thus, similar to mammals, the probability of the chance of escape seems to be a major factor determining the physiological response during freezing immobility in fish. As Volchan et al. (2017) discussed for mammalian cases, freezing should be subdivided into two different immobility states, attentive immobility and immobility under attack. The former is elicited by the detection of a potential threat and is ready to switch to another anti-predator behavior by monitoring the environment.

The latter occurs in case the prey detects signs of imminent attack and tries to reduce the possibility of an actual attack by the predator. The underlying autonomic balance between the two types of freezing behavior in fish has yet to be investigated.

The occurrence of the freezing immobility as an anti-predator behavior varies depending on environmental and physiological conditions. Trinidadian guppies *P. reticulata* inhabiting shallow riffles tend to freeze on the bottom upon potential aerial threat, while guppies inhabiting heavily vegetated streams hide under shelter in response to an aerial threat to reduce the risk of detection (Templeton and Shriner 2004). Male orangethroat darters *E. spectabile* in breeding states are likely to flee and less likely to freeze compared with those in non-breeding states when threatened (Radabaugh 1989). This is suggested to be due to the high-contrast vivid coloration of the male darter in the breeding state that lessens the cryptic effect of body coloration (Radabaugh 1989). The satiation level also affects the tendency to freeze in response to conspecific alarm substances. Although food-deprived Brazilian catfish *Pseudoplatystoma corruscans* show fright responses to exposure to an alarm substance the same as in fed fish, the freezing component of the response is abolished in the hungry fish (Giaquinto and Volpato 2001).

In addition to fear responses, in which the fish detects an apparent cue of a threat, elevated anxiety also elicits freezing immobility as in the case in mammals. Freezing immobility, together with other fear/anxiety-related behaviors, has been well documented for zebrafish in the field of translational neurobehavioral research involving the evaluation of anxiogenic or anxiolytic effects of compounds (Kalueff and Cachat 2011; Kalueff et al. 2012; Kalueff et al. 2013).

11.4 Tonic Immobility

The definition and biological significance of TI in animals in both vertebrates and invertebrates are described in Chap. 1 of this book. In this chapter, I briefly mention the general features of TI in vertebrates (mainly mammals) and introduce cases in fish, for which the biology of TI has been less studied compared with other animal groups.

11.4.1 General Features of TI in Vertebrates

Tonic immobility is a reflexive and involuntary reaction manifesting at the terminal phase of the defense behavior cascade (Kozlowska et al. 2015; Volchan et al. 2017; Kuiling et al. 2019). TI as an anti-predator response is seen in all classes of land vertebrates. This behavior is characterized by a subdued response to sensory stimulation and systemic catalepsy. Cardiac and respiratory decelerations seem to be common in stably sustained phase of TI (McDonald 1974; Nash et al. 1976; Giannico et al. 2014) although it is still controversial. Some studies have reported cardiac acceleration especially during induction period and/or initial phase of the TI (Nash et al. 1976; Gentle et al. 1989; Valance et al. 2008). The increased heart rate is probably due to physical and emotional stress caused by the procedure. Thus, it should be noted that autonomic balance in TI varies depending on the context of the induction and on the course of the TI.

During TI, although unresponsiveness to external stimuli is obvious, the central processing of sensory information appears to be unsuppressed and animals are capable of sensory association (Klemm 1966, 1971; Gallup et al. 1980). Neural substrates involving tonic immobility in mammals are comprehensively reviewed by Klemm (2001). Humans also are aware of their circumstances and retain a memory during TI under extreme threats where no other responses are possible (Kozlowska et al. 2015).

The adaptive value of TI is apparent as distinctively described for ducks and foxes (Sargeant and Eberhardt 1975) and in Japanese quails and cats (Thompson et al. 1981). In the terminal phase of an attack by a predator, the chance of survival of the prey is only expected when the predator loosens its grip or loses interest in the dead prey.

Although TI is apparently a fear-emotion-driven and/or reflexive terminal defensive response widely observed in various land vertebrates elicited usually by physical contact by a predator, there are a couple of cases that stand out from the others. Two famous "death-feigning" TI cases are of *Didelphid* opossums and *Heterodon* snakes as seemingly exaggerated performances. The North American opossum *Didelphis virginiana* shows a characteristic TI response, or death feigning, by violent provocations such as "grab and shake" by hands or by dogs (Francq 1969; Gabrielsen and Smith 1985). Francq (1969) reported that TI can also occur, if not typically, without tactile contact. In such cases, following the freezing response, the animal falls onto its side with a curled body and tail. Typical behavioral features during TI in the American opossum include open eyes, open mouth, extended tongue, salivation, urination, and defecation (Francq 1969; Gabrielsen and Smith 1985). Physiologically, a decrease in heart rate, respiration rate, and body temperature are observed (Gabrielsen and Smith 1985). As a defensive behavior, death feigning in the American opossum appears to be significant, since *"Despite our strongest encouragement, our dog invariably lost interest in the opossum once it entered this* (tonic immobility) *state"* (Gabrielsen and Smith 1985). It should be noted that not all *Didelphis* species show such remarkable death feigning: it is common in *D. virginiana*, rare in *D. albiventris*, and not reported in the others (Hunsaker and Shupe 1977; Kimble 1997).

Hognose snakes, or *Heterodon* species, are another example famous for their remarkable death feigning. Jones (1894) reported the stereotypical death feigning behavior of *Heterodon platirhinos* as follows: *"… at first tried to escape, but on being captured it turned on itself with mouth wide open, head thrown back sharply, and tongue limp and protruding."* During death feigning, the body is quite limp, and notably, when it is turned to the right position, the snake rolls back again and lays on its back. Upon induction of death feigning in *Heterodon* species, a marked bradycardic response has been observed immediately after rolling onto the back (McDonald 1974).

During TI, either elicited by physical contact or by external cues, animals are monitoring the presence of a predator. They apparently use visual information to assess the situation since the gaze by the predator or experimenter prolongs the duration of the immobility compared to just a presence of the threat (Hennig 1977; Gallup et al. 1972; Burghardt and Greene 1988). Given these lines of experimental and empirical evidence, it is almost irresistible to think that the occurrence and/or maintenance of some forms of TI involves intended behavior of the animals.

11.4.2 TI in Fish

Tonic immobility has often been used as a practical technique to keep fish quiet and still during various measurements and manipulations. It has been reported for more than 20 fish species, including both chondrichthyan and actinopterygian fishes, that the TI state is artificially inducible (Whitmann et al. 1986; Henningsen 1994; Brooks et al. 2011; Kessel and Hussey 2015). Quantitative case reports for artificial induction of TI in actinopterygian fishes are relatively scarce, and many of them were published in the early twentieth century (Whitman et al. 1986), compared with the availability of recent reports in chondrichthyans (elasmobranchs), especially the sharks. Since observations of TI in natural conditions are rare, the commonality and significance of TI as a defensive behavior in fish are yet to be determined.

11.4.2.1 Elasmobranchs

Tonic immobility can be artificially induced in most sharks and rays examined to date (Whitman et al. 1986; Henningsen 1994; Brooks et al. 2011; Kessel and Hussey 2015). Quick dorsoventral inversion and holding the fish in this posture for seconds to minutes make the shark act "limp", and the limp response can be an indication of successful induction of the TI state (Whitman et al. 1986). Thus, the condition of the skeletal muscles during TI in sharks is muscular hypotension, contrary to the increase in muscle tension or catalepsy in the case of TI in land vertebrates. Decreased rate of respiration and deep ventilatory movement are other characteristics during TI in elasmobranch fishes (Henningsen 1994). In one case for the Halmahera walking shark *Hemischyllium halmahera*, in addition to inversion, massaging the snout, where ampullae of Lorenzini are densely distributed, can be applied to induce TI although the effectiveness of the massaging has not been verified (Mukharror et al. 2019).

In the zebra shark *Stegostoma fasciatum*, it is known that TI is immediately induced by applying pressure to or grabbing the distal end of the tail (Henningsen 1994; Williamson et al. 2018). It has been suggested that the induction of the immobility state in zebra sharks is used in courtship where biting of the distal end of the

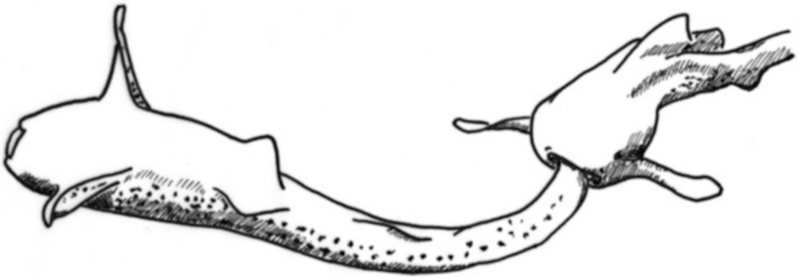

Fig. 11.3 Tonic immobility in a female zebra shark (left) induced by tail biting by a male (right) during courtship. Adapted from Fig. 1 in Williamson et al. (2018): Creative Commons Attribution 4.0 International License (http://creativecommons.org/licenses/by/4.0/)

female's tale by the male makes the female enter a state of immobility (Williamson et al. 2018) (Fig. 11.3). However, as Williamson et al. (2018) reported, no differentiation in this type of immobility reaction between the sexes was found.

In the zebra shark, TI, other than in situations of courtship behavior, possibly functions as an anti-predator defense as in other taxa, because the distal end of the remarkably long tail fin would be a likely place for predator attack, and pressure to this part can induce TI (Williamson et al. 2018). However, the case of the zebra shark is exceptional. In other sharks, dorsoventral inversion and holding the posture for tens of seconds is the usual way to induce TI. In predatory attacks, it seems unlikely for an adult shark to be kept dorsoventrally inverted for such a long period, reducing the adaptive value of the immobility as a terminal defense, although when attacked by a predator, strong and forcible restraint might enhance the induction of TI. Thus, the significance of TI in elasmobranchs, especially sharks, is not yet clear.

Nevertheless, the significance of TI in sharks is obvious from a practical point of view. Artificially induced TI in sharks provides us with a time window for various measurements and manipulations such as the implantation of transmitters (Holland et al. 1999). Kessel and Hussey (2015) have argued for the benefits of TI over chemical-based anesthetics for sharks, especially in the field. In the field, it is obviously impractical to use a chemical anesthetic agent to obtain sufficient depth (stage IIb or III in the stages of anesthesia (McFarland 1959)) for surgery of large aquatic vertebrates. In contrast, the induction of TI requires a relatively short period of postural restraint, and the instant recovery from the immobility state reduces post-release risks (Kessel and Hussey 2015).

Cardiac deceleration during tonic immobility in sharks has been shown to be associated with, and caused by, a decrease in ventilation, indicating that the integrity of the brainstem controlling cardiorespiratory function is kept intact during TI (Davie et al. 1993). Although physiological perturbations associated with the disruption of respiration, which can be compensated for by artificial irrigation of the gills, are not negligible (Brooks et al. 2011), the negative effects of TI appear to be acceptable compared to anesthesia by chemical agents.

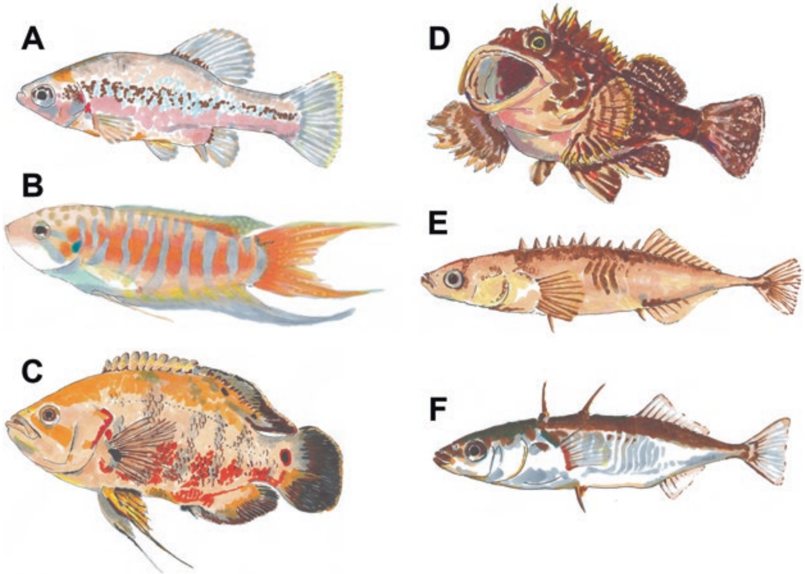

Fig. 11.4 Some fish species that show tonic immobility as a defense behavior. (**a**) butterfly splitfin *Ameca splendens*. (**b**) Paradisefish *Macropodus opercularis*. (**c**) Oscar *Astronotus ocellatus*. (**d**) A rockfish *Sebastiscus marmoratus* showing a resistive rigid posture. (**e**) Ten-spined stickleback (aka ninespine sticklepack) *Pungitius pungitius*. (**f**) Three-spined stickleback (aka threespine stickleback) *Gasterosteus aculeatus*. Reference materials were partly given by courtesy of Kamihata Fish Industries LTD

11.4.2.2 Teleosts

Tonic immobility caused by mimicked predatory attack or in high anxiogenic situations has been reported for the juvenile butterfly splitfin *Ameca splendens* (Goodeidae) (Fitzsimons 1973), paradisefish *Macropodus opercularis* (Osphronemidae) (Kabai and Csányi 1978), and oscar *Astronotus ocellatus* (Cichlidae) (Crawford 1977) (Fig. 11.4a, b, and c). TI is easily inducible in all of these species by an abrupt approach of a potentially threatening object like a human hand. For butterfly splitfin and paradisefish, introducing the fish into a novel tank, which is a highly anxiogenic situation, has been reported to be enough to induce TI. However, Kabai and Csányi (1978) described that immobility in paradise fish is often interrupted for a few seconds by intensive tail beats, suggesting that the immobility in this situation is a variation of freezing behavior, which is commonly intermitted by short periods of erratic movements (see above). Tonic immobility induced by a visual threat or other stressful events in oscars more resembles artificially induced TI in sharks. Oscars in a state of TI show slow and deep respiration (Crawford 1977).

For the juvenile butterfly splitfin, the significance of TI as a defense behavior is clear from fish showing TI surviving longer in the presence of predatory fish than individuals showing less TI behavior although detailed information is not available (Fitzsimons 1973). In this species, the posture of the immobility is characterized by systemic rigidity including a widely opened operculum, full expansion of the paired and median fins, strongly curved body, and mouth gape (Fitzsimons 1973). Thus, it can be said that the function of the TI in the splitfin is similar to that in the toadfish as described below.

Another notable case of the IT in teleost fish has been reported for Brazilian seahorses *Hippocampus reidi* (Freret-Meurer et al. 2017). In this species, TI was induced by a manipulation of the individuals by hands of the experimenter, either in the field or in the laboratory. During the immobility, seahorses rigidly curled their head and tails toward the abdomens, while some of the laboratory-kept individuals showed a stretched posture, and no breathing or eye movements were observed (Freret-Meurer et al. 2017). As swimming ability of seahorses is limited and they are not powerfully armed, a functional meaning of the immobility in the seahorses in threatening condition is probably identical to that in generally observed TI in insects: avoiding further attack by a predator. Since only a small portion of the individuals showed such characteristic TI postures in response to the handling (5 of 342 and 3 of 66 individuals in the field and in the laboratory, respectively), it is yet to be determined that this response is common in seahorses in the situation of actual predatory attack.

The toadfish *Opsanus beta* (Batrachoididae) shows a similar rigid posture including stiffened fins and maximally distended operculum in response to potentially threatening visual stimuli (Gunter and McCaughan 1959). Although the authors mention this immobility posture as a cataleptic state, the heightened systemic muscular tonus would have a tendency to repel external mechanical force. Many rock-dwelling scorpaeniform fishes show similar behavioral responses against predatory attack (Fig. 11.4d). Although this response is considered to be a defensive behavior, the function is unlikely to be the same as that of TI in many other vertebrates. Rigidly erected spiny fins and a widely opened thorny operculum would make a predator hesitate to further attack or ingest, and when the prey fish is in a gap or crack among rocks, the posture helps to resist an attempt by the predator to pull the prey out. An effectiveness of rigid postures with elected spines in prey fishes against consumption by a predator has been demonstrated in sticklebacks *Gasterosteus aculeatus* and *Pygosteus pungitius* (syn. *Pungitius pungitius*) (Hoogland et al. 1956) (Fig. 11.4e, f). When seized by a predator, a pike *Perca fluviatilis* or a perch *Esox lucius* in this case, sticklebacks rigidly erect their spines and keep motionless. The predator rejects the prey, and, after a small number of experiences eventually become negatively conditioned to avoid the sticklebacks (Hoogland et al. 1956). Supportedly, three-spined stickleback *G. aculeatus*, which have large stiff spines, is superior in the protection than ten-spined stickleback *P. pungitius* having smaller spines (Hoogland et al. 1956). In these context, this type of immobility posture in fish shares features with the death feigning posture in the pygmy grasshopper *Criotettix japonicus* (Honma et al. 2006; Chap. 3 in this book). Rigid spiny shapes, however, may not always protect the prey animals, and the validity apparently depends on its shape and relative size of the prey animals. Nishino and Sakai (1996) have reported that crickets showing TI in the mouth of a lizard were not rejected even though the crickets possess spines on the legs. Even from a limited number of observations, the manifestation of TI induced by threatening situations varies depending on teleost species. Limited information of physiological conditions during those immobility states makes it difficult to compare further with land vertebrates.

As in elasmobranchs, TI can be induced in the teleost goldfish *Carassius auratus* by quick dorsoventral inversion and firm restraint for tens of seconds (Davis and Holmes 1971; Yoshida unpublished) (Fig. 11.5). Gentle, rhythmic strokes with the fingertips in the area of the anterior abdomen facilitate the induction of immobility (Davis and Holmes 1971). Applying mild pressure to the anterior abdomen is also effective.

An apparent limp response is seen in goldfish during induced immobility, and the muscular tonus is greatly reduced. During TI, goldfish is obviously capable of sensing external stimuli, since the fish responds to arousing events such as tactile and visual stimuli with phasic reduction in ventilatory frequency although righting or escaping movements are not elicited. Furthermore, classical conditioned respiratory deceleration is achieved even in the immobility state (Davis and Holmes 1971), indicating basic central circuits involving sensory processing and association with stimuli are kept intact even during induced TI (Table 11.1).

Generally, catalepsy is not apparent in fish during TI. Rather, a limp response is characteristically observed in TI in both elasmobranchs and teleosts induced by postural manipulation and restraint, which are also commonly used to induce TI in land vertebrates.

11.4.2.3 Death and Illness Feigning in Fish as a Hunting Tactic

So far, there are three species that have definitely been reported to show death or illness feigning as a part of predatory behavior (McKaye 1981; Gibran 2004; Tobler 2005). The first quantitative description of death feigning was done for the African

Fig. 11.5 Induced tonic immobility in goldfish. The goldfish was placed in a V-shaped holder with a dorsoventrally inverted posture and restrained for tens of seconds to induce a tonic immobility state

Table 11.1 Summarized features of three types of immobility behaviors in vertebrates

	Primary defense		Secondary defense
	Orienting immobility	Freezing immobility	Tonic immobility
Situation	Detection of unfamiliar signs	Detection of an actual threat	Imminent attack or physical contact by a predator
Behavior	Stabilized, upright posture	Motionless, tense crouching	Lying Unresponsiveness to external stimuli[a]
Physiology	Facilitation of sensory system Increased muscle tone Decrease in heart/respiration rate	Facilitation of sensory system Increased muscle tone Decrease or increase in heart/respiration rate[c]	Paralysis[b] Decrease in heart/respiration rate[d]
Major function	Maximizing the monitoring of the environment	Minimizing the detection by a predator	Suppression of further attack by a predator

[a] Central processing of sensory information is ongoing

[b] Catalepsy is common in mammals; accompanying "limp" or rigid posture in fishes

[c] Varies depending on animal species and the context (see Sect. 11.3.1)

[d] Beginning of TI frequently accompanies cardiac acceleration (see Sect. 11.4.1)

cichlid *Nimbochromis livingstonii* (McKaye 1981). This predatory cichlid drops through the water column to the bottom and lays on its side, and occasionally its abdomen is buried partially in the sand. The behavior and color pattern of *N. livingstonii* mimic a dead fish and attract scavenging small fishes, which are potential prey of this predatory cichlid (McKaye 1981).

The Central American cichlid *Parachromis friedrichsthalii* has also been observed to show death feigning (Tobler 2005). Upon feigning death, *P. friedrichsthalii* sink to the bottom slowly and turn over on their side. Scavenging fishes are attracted by this death feigning fish and even pick on the body, making the fins frayed (Tobler 2005). Attack of the predator occurs when the small scavenging fish comes close enough. Tobler (2005) has suggested that feigning death hunting strategies have evolved at least twice within the cichlids; in Africa and in Central America.

In addition to the two freshwater species, a marine species, the comb grouper *Mycteroperca acutirostris* that inhabits southwestern Atlantic coastal waters, has been reported to show death/illness feigning (Gibran 2004). In limited sightings of the feigning, a juvenile comb grouper lays on its side on the bottom with occasional undulating of its body, apparently mimicking an ill or injured state (Gibran 2004). This death/illness feigning is successful enough to attract small fish, some of which are eventually captured by the predator (Gibran 2004).

Feigning death or illness as a hunting strategy is probably related to ambush and stalking tactics (Gibran 2004; Tobler 2005). In clear water, without cover for ambushing or stalking, it is difficult for a predator to approach its prey, and hence such an environment might promote the evolution of alternative hunting strategies like death or illness feigning to attract prey to within range of successful attack (Gibran 2004, Tobler 2005).

11.5 Significance of Immobility Behaviors in Fish

The adaptive significance of some immobility behaviors that manifest during orienting and freezing in the course of the defense cascade in fish is apparent as in other vertebrates. Orienting immobility maximizes information gathering and the assessment of the seriousness of a threat. Freezing immobility minimizes the possibility of detection by a predator while the animal continues to monitor the environment and wait for an opportunity to flee or hide. However, the adaptiveness of TI is not always clear when it comes to defensive mechanisms prevalently used in various fish species. That is partly due to the limited observations of TI in the terminal phase of the defensive cascade.

Fear emotion underlies multiple steps in the defense cascade: as the fear level increases, the cascade proceeds (Marx et al. 2008). Tonic immobility, including that in humans, is probably one form of emotional expression associated with extreme fear although the involvement of reflexive components cannot be excluded. The method of artificial induction of TI in fish is similar to that which is effective for land vertebrates: quick dorsoventral inversion and restraint, suggesting that the contribution of the reflexive component in TI induction is conserved through vertebrate evolution.

In the case of fish, however, TI that is functionally identical to that in land vertebrates might not be common. Many predatory fish suck a prey as a whole in one gulp, and hence limped, not cataleptic, musculatures as seen in artificially induced TI is unlikely to work in the natural environment. Immobility of a prey fish after attack can even facilitate the adjustment of the direction and ingestion by predators including birds. In this respect, the rigid thorny/spiny posture of some rockfishes and sticklebacks facing a threat is likely to be adaptive anti-predator behavior although this behavior can occur even in the early phase on encountering a predator.

Death or illness feigning in some predatory fish to attract small prey fish is another immobility-like behavior that is probably a form of an elaborated ambush or stalking tactic.

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