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# Antipredator tactics: A kin-selection benefit for defensive spines in coral catfish?

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**Abstract**

Morphological features that impair a predator's ability to consume a prey item may benefit individual prey; but what of features that prolong prey-handling but do not enhance prey survival? For example, a Striped Eel Catfish (*Plotosus lineatus*) will be fatally envenomated if struck by its specialist predator, the Greater Sea Snake (*Hydrophis major*). Nonetheless, the catfish typically erects long, toxic pectoral and dorsal spines that increase prey-handling times for the snake by around eightfold. Because the catfish travel in swarms of closely-related individuals, the delay enforced by spines may enable the victim's swarm-mates to disperse before the snake is able to search for another meal. In keeping with that hypothesis, defensive spines tend to be longer in catfish from regions where the Greater Sea Snake occurs, than from areas where the snake does not occur. Our data thus suggest that defensive weaponry in catfish, as in some eusocial insects, can evolve via kin selection as well as natural selection.

Keywords: antipredator, marine, Olive-headed Sea Snake, hydrophiine, predator-prey

## Introduction

Mortality due to predation is an important influence on lifetime reproductive success in many taxa, favouring the evolution of diverse antipredator tactics (e.g. Mori and Ito 2017). One major mechanism is the elaboration of morphological features that render a prey item difficult to ingest – for example, by inflating the body with air (Ferreira et al. 2019), or the production of mucus (Gould et al. 2019) or toxins (Brodie et al. 1991), or the development of sharp spines that increase effective prey size and render ingestion hazardous (Shepherd et al. 2019). Such mechanisms presumably increase an individual's probability of surviving an encounter with a predator: a well-defended prey item may be ignored, or rejected after the initial strike, or may escape during a prolonged attempt at ingestion (Gawryszewski 2017). But that explanation is not tenable for antipredator mechanisms that do not enhance the probability of survival of the individual under attack. For example, a worker bee that stings an attacker will die (Nouvian et al. 2016). Such cases have been attributed to kin selection, whereby the damage inflicted by the doomed individual enhances its inclusive fitness via benefits to closely-related individuals (discouraging the predator from targeting the victim's nestmates: e.g. Strassmann and Queller 1989). Our studies of sea snakes and catfish suggest that a similar kin-selection process may operate within vertebrates as well.

Many prey species have evolved defensive spines that discourage and/or impede predators (e.g. Burr and Stoeckel 1999). One of the most impressive examples involves the pectoral and dorsal spines of catfish, that can be locked into an erect position at right angles to the fish's body (Fine et al. 1997, Fine and Ladich 2003). That erect position is maintained even after the fish is killed (Fine et al. 1997).

Combined with toxic skin secretions that are delivered by those spines (Wright 2009), a predator that attempts to ingest a catfish can be killed or incapacitated if it attempts to ingest such a formidable prey item (Halstead 1978, Halstead et al. 1990). Importantly, the erect spines massively increase the effective size of the prey item, rendering it more difficult to ingest by a gape-limited predator (i.e., an animal that must swallow the prey item whole rather than tearing it into smaller pieces: Fine et al. 2011a). Some taxa of catfish appear to be winning this predator-prey arms race, because their spines make adult catfish invulnerable to most predators (Pimental et al. 1985, Sismour et al. 2013).

Nonetheless, a few predators have evolved to specialize on a catfish diet. One of these is the Greater Sea Snake (*Hydrophis major*) which (at least in New Caledonia) appears to feed exclusively on Striped

Eel Catfish *Plotosus lineatus* (Shine et al. 2019). The snake's powerful venom rapidly kills any fish that is seized (present study), removing any advantage of defensive spines to the individual fish. The prey item is dead, regardless of how difficult it may be to swallow. Why, then, do these catfish have such large spines? Unusually, these catfish travel in schools of closely-related individuals (including siblings: Moriuchi and Dotsu 1973; Matsumura et al. 2004). A delay in prey-handling may afford those swarm-mates an opportunity to disperse from the capture site and thus, evade subsequent attacks by the same predator.

Our arguments about evolutionary forces apply to the length of defensive spines in catfish, not to the initial evolution of traits such as spines, spine-locking mechanisms, and toxins. Those traits are widely distributed among catfish species, including many taxa that do not occur in kin groups (e.g. Halstead 1978, Fine and Ladich 2003). Also, most predators that attack catfish are not toxic and hence, an unsuccessful attack may result in survival of the intended prey item. Individual advantage provides the most parsimonious explanation for the origin and maintenance of weaponry among catfish as a lineage.

Specific features of the predator-prey system that we studied (reviewed below) suggest that elongation of spines may not enhance the fitness of individual catfish, leaving the possibility that this trait has been elaborated by kin selection (giving swarm-mates more time to escape from a predator). To explore the hypothesis that kin selection has affected the evolution of spine size, we test assumptions underpinning that interpretation (e.g. that spines increase handling time) and we test the prediction that spine size will be longer in areas where the catfish are sympatric with the specialist predator than in areas where the snake does not occur.

## Methods

### Study system

*Hydrophis major* (Greater Sea Snake or Olive-headed Sea Snake) is a large hydrophiine elapid snake (to 1.5 m body length) that is distributed along tropical and subtropical coasts of Australia, southern New Guinea, and some Pacific Islands (Heatwole and Cogger 1994). Older studies of *H. major* from a range of localities reported a wide array of fish species within the diet, but recent observations of feeding by free-ranging specimens in New Caledonia, and records of prey items in dissected specimens in Australian

museum collections, have involved only a single species of fish: the Striped Eel Catfish *Plotosus lineatus* (N = 24 records: Letourneur and Briand 2012; Shine et al. 2019).

The catfish *Plotosus lineatus* has a wider geographic distribution than does *H. major*, being recorded from tropical and subtropical oceans from Madagascar to Indonesia as well as Australia, and from southern as well as northern coasts of the latter continent (Clark et al. 2011). The species also has invasive populations in the Mediterranean (Ali et al. 2015). It is one of the only catfish species recorded from coral-reef habitats (e.g. Cameron 2012). The fertilized eggs are brooded by the adult male until hatching, and the siblings form into tight aggregations within a few days of hatching, and begin to move about as a school (Moriuchi and Dotsu 1973, as *P. anguillaris*). Experimental studies have shown that catfish of this species are attracted to chemical cues from their own school, maintaining the kin structure of those aggregations (Hayashi et al. 1994). Those schools persist throughout juvenile life, although multiple clutches sometimes coalesce to form large swarms (Clark et al. 2011). In the field, swarms of catfish have been recorded to move hundreds of meters in an hour (Clark et al. 2011). The distances moved may be affected by interactions with predators: in another species of catfish, chemical cues released by predators and injured conspecifics induced juvenile catfish to flee (Coulter 2013, Vogel et al. 2017). After they reach adult size, Striped Eel Catfish become more solitary (Clark et al. 2011); the sizes of catfish eaten by Greater Sea Snakes confirm that they feed on both swarming and solitary individuals (Shine et al. 2019, present study).

Like many catfish, *P. lineatus* possess long spines beside their pectoral and dorsal fins. These sharp barbed spines can be erected if the catfish is attacked, and slot into bony notches that hold them in place (at right angles to the fish's body) even after the fish is killed (Fine et al. 2011a). The spines likely evolved as a defence against gape-limited predators (Fine et al. 2011a), because they massively increase the physical challenge faced by any predator that attempts to ingest them. For example, at the mean body size of the New Caledonia specimens that we examined (length 106 mm, mass 7.4 g), the body at the widest part averaged  $14.6 \times 15.6$  mm; but with spines erected, the effective "prey size" increased to  $27.6 \times 31$  mm (i.e. the cross-sectional area increased fourfold, from  $176.6 \text{ mm}^2$  to  $707 \text{ mm}^2$ ). The spines also deliver a potent toxin, capable of causing extreme pain and in extreme cases, of killing a human being (Halstead 1978). Perhaps because of these formidable defences, *P. lineatus* are eaten by very few predators; the only record in the massive online database Fishbase (<https://www.fishbase.se/summary/Plotosus-lineatus.html>; accessed 14 March 2020) is a single case of

ingestion of *P. lineatus* by a flathead (*Platycephalus indicus*). A study on captive sea snakes (*Hydrophis cyanocinctus*) reported feeding the snakes on *Plotosus lineatus* (Karthikeyan et al. 2008), but the only published records of this catfish genus being consumed by sea snakes in the wild other than by *H. major* (see above) come from the extensive review by Glodek and Voris (1982): they recorded the closely related *P. canius* in the diets of *Enhydrina schistosa* (N = 21 records), *Hydrophis ornatus* (N = 1) and *H. hardwickii* (N = 1).

### Field observations

In the course of fieldwork on sea snakes in the Baie des Citrons, we snorkelled regularly through this small bay beside the city of Noumea in the Pacific archipelago of New Caledonia (see Goiran et al. 2020 for a description of this site). In the process, we sometimes encountered *Hydrophis major*. Whenever we saw a snake seize a catfish or (more commonly) saw a snake manipulating and swallowing a catfish, throughout 2018 through to 2020, we photographically recorded those interactions (see Fig. 1; and Supplementary material Appendix 1, Video A1, Video A2).

### Prey-handling times

We captured five Greater Sea Snakes (snout-vent lengths 53 to 130 cm) by hand from the Baie des Citrons over the period 14 to 21 January 2020. Each snake was immediately transferred to a large tank (2 × 2 m, 18 cm deep) with flow-through seawater in the nearby Aquarium des Lagons. Catfish (N = 42, body lengths 70 to 123 mm) were collected in nearby bays, and maintained at the Aquarium until use. We allowed some snakes to capture and kill catfish, but (for ethical reasons, and to minimize confounding factors) most fish were killed by us before they were presented to the snake on forceps. We killed the fish in one of two ways: a sharp blow to the top of the head (which resulted in spines being erected and locked into place) and immersion in near-freezing seawater (which resulted in spines remaining folded against the fish's body). Each snake was presented with catfish with spines either erect or not, in random order (total of 10 trials), plus an additional 12 trials (6 with spines erect, 6 with spines folded) using snakes that were held in captivity for slightly longer periods than other animals (allowing replication of tests).

To quantify handling time, we divided the prey-ingestion sequence into two components: (1) prey manipulation (initial strike until the fish was positioned head-on to the snake, ready for swallowing); and

(2) swallowing (from the time the fish was positioned until it was no longer visible outside the snake's mouth). Trials were videotaped, and times recorded from the video playbacks.

### **Morphology of catfish**

We used a stainless-steel ruler ( $\pm 1$  mm) to measure body length, maximum body diameter (based on measurement of maximum height and width of the trunk at the thickest part of the body, near the pectoral fins) and length of pectoral and dorsal spines in freshly-killed catfish at the Aquarium des Lagons in Noumea (N = 20), and preserved specimens in museum collections of the Australian Museum (N = 156) and the Museum and Art Gallery of the Northern Territory (N = 18).

### **Statistical methods**

Data on prey-handling and swallowing times were ln-transformed to achieve normality and variance homogeneity. To quantify relative spine length, we regressed mean spine length (mean of pectoral and dorsal spine lengths) against maximum body width (mean of height and width at the widest part of the body) in a general linear regression, and calculated residual scores. A positive residual score indicates a fish with longer-than-average spines for its body width. Analyses using body length as the independent variable in that regression yielded results almost identical to those based on body width.

We compared prey-handling times when snakes were given fish with spines erected versus not erected, using repeated-measures ANOVA (in JMP 13.0) with ln-handling times with and without erect spines as the repeated measure (dependent variable) and snake ID as an independent variable (the latter included to prevent pseudoreplication). To compare relative spine lengths (residual scores) among catfish collected from different geographic areas, we scored each site in terms of sympatry with Greater Sea Snakes. Five sites were outside the snake's range (Lord Howe Island, Norfolk Island, Asia, New South Wales, Madagascar), and four were within the snake's range (tropical Western Australia, Northern Territory, Vanuatu, and New Caledonia). A further two sites (Papua New Guinea and Queensland) included sites with and without the sea snake species, so we scored them as "partially sympatric". We used a random-effects ANOVA to analyse the data on residual spine lengths, with factors being the sympatry category, and site (a random factor) nested within the sympatry category.



## Results

### Field observations

In the course of fieldwork in the Baie des Citrons beside Noumea, we have photographed *H. major* seize, manipulate and swallow Striped Eel Catfish on five occasions. Most of those observations were photographed, allowing us to determine that the formidable pectoral and dorsal spines of the catfish were erect on at least four of these cases. Even in the case when the spines were not fully erect, they impaired feeding by impaling the snake's body, causing it to writhe around to free the barbs from its scales. All catfish were swallowed head-first, and the school of catfish tended to remain in place while the snake drifted away as it swallowed the fish it had seized (Supplementary material Appendix 1, Video A1, Video A2).

### Prey-handling times

All five *Hydrophis major* immediately seized and consumed the catfish that we offered to them. They struck the catfish (usually in the posterior part of the body) and retained their grip until the fish stopped struggling (typically within a minute or two), then “jaw-walked” to transfer their grip to the fish's head so that the prey could be swallowed head-first. Ingestion did not begin until the prey had ceased all movement. The catfish spines were erected and locked into place in 2 of 4 cases in which the fish was killed by the snake rather than pre-killed by us. In all five snakes tested, catfish with erect spines required longer to manipulate and to swallow than did catfish with spines that were not erected (combining data for fish that were killed by snakes and those that were pre-killed by us:  $N = 11$  cases with erect spines,  $N = 11$  cases with folded spines; handling time – means 536.91 seconds (range 38 to 1556 sec) vs. 92.3 seconds (range 10 to 354 sec);  $F_{1,6} = 10.42$ ,  $p < 0.02$ ; swallowing time – means 169.36 (17 to 500) vs. 26.9 (5 to 117) seconds;  $F_{1,6} = 8.90$ ,  $p < .02$ ; see Fig. 2). The delay in prey manipulation was due to the erect spines embedding in the snake's body, whereas the delay in swallowing reflected the erect spine-tip impaling tissue within the snake's mouth (inducing bleeding in at least two cases). All snakes recommenced prey-searching immediately after consuming a fish, and ate as many as we offered them (up to four catfish within 30 minutes).

### Morphology of catfish

Relative to body length, length of the defensive spines averaged 7.0% and ranged from 5.5% (Lord Howe Island) to 10.4% (New Caledonia) among the 11 regions for which data were available. Relative to maximum body width, spine length averaged 47.6% and ranged from 33.4% (Lord Howe Island) to 74.1% (New Caledonia). Thus, the range in mean spine lengths (relative to body size) was approximately twofold across regions. Mean values for spine length of catfish from sites allopatric, partially sympatric, and sympatric with Greater Sea Snakes were 39.9, 55.0 and 70.6% relative to body width, and 6.1, 7.4 and 9.9% relative to body length. Statistical analysis based on residual scores showed that mean spine lengths relative to body width varied significantly among these categories ( $F_{2,12.61} = 6.06$ ,  $p < 0.015$ ). A Tukey post-hoc test showed that catfish from areas of complete sympatry with Greater Sea Snakes had longer spines than did conspecifics from areas where these snakes do not occur ( $p < 0.05$ ). Relative to body length (rather than width), the three categories for sympatry also differed ( $F_{2,11.8} = 6.96$ ,  $p < 0.011$ ), with sympatric *versus* allopatric populations significantly different from each other in a post-hoc test. Nonetheless, the correlation between sea snake presence and catfish spine length is not perfect; for example, catfish from one site which lacks sea snakes (Norfolk Island) had spines as long as those of conspecifics from some locations where sea snakes occur (Fig. 3).

## Discussion

Hollywood movies often include a scene where the fatally wounded hero continues to fight off the foe for as long as possible to allow his family time to escape. We suggest that the defensive spines of Striped Eel Catfish may be under selection through the same mechanism. That is, longer spines do not enhance survival of the individual prey item (because it has already been killed by the snake's venom) but nonetheless increase that individual's inclusive fitness via kin selection.

Specific features of the predator-prey system permit a natural experiment to test the kin-selection hypothesis:

- (1) prey will not survive even if they escape after the initial strike, because they are badly injured (especially likely if the predator is highly toxic);

- (2) the predator is gape-limited, so that morphological features of the prey (spines) can substantially increase handling time;
- (3) the predator is highly specialized to consume this prey species, and few if any others;
- (4) the antipredator features (defensive spines) lock into position, such that they remain effective even after the individual prey item dies;
- (5) prey size is small relative to predator size, such that a single predator will consume multiple prey items in quick succession if given the opportunity to do so;
- (6) the prey species lives in mobile swarms of closely related individuals, in an environment where water currents may render it difficult for a predator to relocate a swarm if sufficient time elapses;
- (7) the weaponry of the prey species (long sharp toxic spines) renders it safe from most predators, increasing the importance of this specialist predator as a selective force on antipredator tactics of the prey;
- (8) the geographic range of the prey is wider than that of its specialist predator, enabling us to compare weaponry in prey that are allopatric versus sympatric with that predator.

Several features of our results agree with published reports of predator-prey interactions. For example, catfish spines have been reported to injure snakes that try to eat these fish (Burr and Stoeckel 1999) and to impede attempts at ingestion (Voris et al. 1978). Nonetheless, the combination of attributes summarized above will not apply to most other predator-prey systems, even within the same habitats. For example, most marine fishes have pelagic larvae, such that juveniles are solitary or occur in schools of distantly-related juveniles (Doherty et al. 1985). Kin selection would not favour adaptations to prolong prey-handling in that circumstance. Likewise, there is no need to invoke kin selection if defensive spines enhance survival of an individual prey item. For example, the spines of catfish increase their probability of surviving attempted ingestion by nonvenomous predators such as largemouth bass (Bosher et al. 2006, Fine et al. 2011a). In such a system, the most parsimonious explanation for the evolution of antipredator weaponry is advantage to the individual rather than to its relatives (e.g. Williams 1966).

Traits such as spines, spine-locking mechanisms, and toxins are widely distributed among catfish, and presumably evolved because they confer an advantage to an individual fish that is attacked by a predator (e.g. Halstead 1978, Fine and Ladich 2003). In the case of a Striped Eel Catfish seized by a Greater Sea Snake, however, the selective advantage of resisting ingestion is minimal (the catfish is killed by immediate envenomation after the initial strike) whereas the benefit to the victim's siblings may be substantial (a predator that takes several minutes to consume the prey item may fail to relocate the

swarm). To test this idea more robustly, we need to observe interactions between snakes and catfish in the field. Our videos (Supplementary material Appendix 1, Video A1, Video A2) suggest that catfish swarms generally remain in place during the time that a snake is swallowing a recently-captured fish, but we did not continue observations long enough to know if the predator (which by then had usually drifted several metres from the sedentary swarm) managed to relocate the swarm. To test our hypothesis, we need to know how often a snake manages to relocate a catfish swarm from which it has previously seized a prey item, as a function of the time required to handle and ingest the initial prey item. Also, does relatedness among catfish within a single swarm remain high through time, or does the initially high relatedness (i.e. all founding members of the same swarm are siblings) decrease through exchange of individuals over the following weeks and months (despite swarm-specific attractant cues: Moriuchi and Dotsu 1973, Hayashi et al. 1994, Clark et al. 2011)? Our critical inference of high relatedness among individuals within a catfish swarm is based on a study of a single clutch within a laboratory setting (Moriuchi and Dotsu 1973), and data on relatedness of individuals within and among free-swimming swarms of catfish would be of great interest.

There are two ways in which prolonging prey-manipulation times might be favoured by kin selection. The first possibility is the one that we have explained above: prolonged ingestion reduces the predator's ability to find and kill siblings of the initial prey item. A second possibility is that the difficulty of ingesting a well-defended prey item might discourage predators from attacking such items in future, thereby protecting conspecifics (i.e. intraspecific mimicry). In keeping with that hypothesis, predatory bass learn not to attack Channel Catfish if less-well-defended prey types are available (Fine et al. 2011b, Sismour et al. 2013). However, that second hypothesis cannot apply if the predator in question feeds exclusively on the well-defended taxon, as is the case with our study system. Greater Sea Snakes eat only this single species of catfish (at least in New Caledonia: Shine et al. 2019) and hence, cannot shift to other prey taxa in response to the challenge imposed by catfish weaponry.

If the prey species in question is consumed by few other predators, but is the sole dietary item for a specialist predator (as is the case in this system), we might expect selection on spine lengths to be greater in sites where the specialist predator is more abundant. Consistent with that prediction, defensive spines tended to be longer in regions where the catfish is sympatric with Greater Sea Snakes, than in sites where the predator is not found (see Fig. 3). Also consistent with our data, Ali et al. (2015) reported relatively short spines (5 to 6% of body length) in two catfish specimens from Mediterranean waters (and thus,

allopatric with the sea snakes). We lack the data to test the prediction about geographic patterns of spine lengths versus predation risk more precisely, because we have no information on densities of snakes or of other predators, nor on the importance of catfish in the diets of Greater Sea Snakes in any given area. Snakes in Western Australia and the Northern Territory appear to have broader diets than do conspecifics in New Caledonia (Shine et al. 2019) and also, catfish in the former areas have shorter spines (Fig. 3). The correlation we highlight here between length of defensive spines and sympatry with Greater Sea Snakes (albeit imperfect) suggests that longer spines confer some disadvantage in sites where predation pressure is low – otherwise, we might expect to see long spines retained in all areas. The most plausible “cost” involves hydrodynamics. Minor variations in the shape of fins and spines can affect hydrodynamic drag (e.g. Lauder and Drucker 2004; Kawabata et al. 2014), increasing costs of locomotion. In populations of channel catfish maintained in captivity over several generations (and thus, no longer exposed to predators), the length of defensive spines exhibited a rapid decrease that was caused by adaptation rather than by phenotypic plasticity (Duvall 2007, Fine et al. 2011a, 2014). In another fish species (the stickleback), defensive spines are longer in populations exposed to gape-limited predators (Huntingford and Coyle 2007).

In summary, our data support critical assumptions and predictions of the hypothesis that the length of defensive spines in Striped Eel Catfish is under kin selection. Longer spines may have evolved not to enhance the survival of individuals seized by a predator, but to prolong prey-handling and thus, reduce the likelihood that siblings of the bitten individual will be attacked as well. The logistical challenges of convincingly supporting or refuting the kin-selection hypothesis in this study system are substantial, however. Working with a large, uncommon, dangerously venomous snake that is highly mobile and lives underwater, makes it difficult to test more sophisticated predictions such as the relative predation success of snakes confronted with swarms of catfish that have short versus long spines. Future work could usefully explore predator-prey interactions in this system in more detail, by observing foraging snakes over long periods of time; and also, could examine antipredator defences in other taxa that occur in sibling groups, to see if kin selection plays a larger role in predator-prey than has been generally believed.

#### **Data availability statement**

Data for the analyses will be stored on the Dryad Digital Repository.

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Supplementary material (available online as Appendix oik-XXXXXX at  
<[www.oikosjournal.org/appendix/oik-XXXXXX](http://www.oikosjournal.org/appendix/oik-XXXXXX)>). Appendix 1 (Video A1, Video A2).

## Supplementary material

OIK-XXXXX

XXX, YYY and ZZZ. 2020. Antipredator tactics: A kin-selection benefit for defensive spines in coral catfish? – Oikos doi: 10.1111/oik.XXXXX

### Appendix 1

Video A1. Video of free-ranging Greater Sea Snake (*Hydrophis major* “Diane”) consuming catfish (*Plotosus lineatus*) in the Baie des Citrons, Noumea. Note that although spines are not erect, the fish’s left pectoral spine impales the snake’s body and prolongs prey-handling. Video credit XXX.

Video A2. Video of captive Greater Sea Snake (*Hydrophis major* “Margali”) consuming catfish (*Plotosus lineatus*). Note that erect spines impede the snake’s attempt to ingest the catfish. Video credit XXX.

**Figure Legends**

Figure 1. (A) Greater Sea Snake (*Hydrophis major*) consuming Striped Eel Catfish (*Plotosus lineatus*) with erect dorsal and pectoral spines, photographed in the wild; (B) erect spines in *P. lineatus* from New Caledonia, showing spine size relative to fish body size. Photographs by XXX (A) and YYY (B). In panel (B), red arrows point to pectoral spines, and black arrow points to dorsal spine.

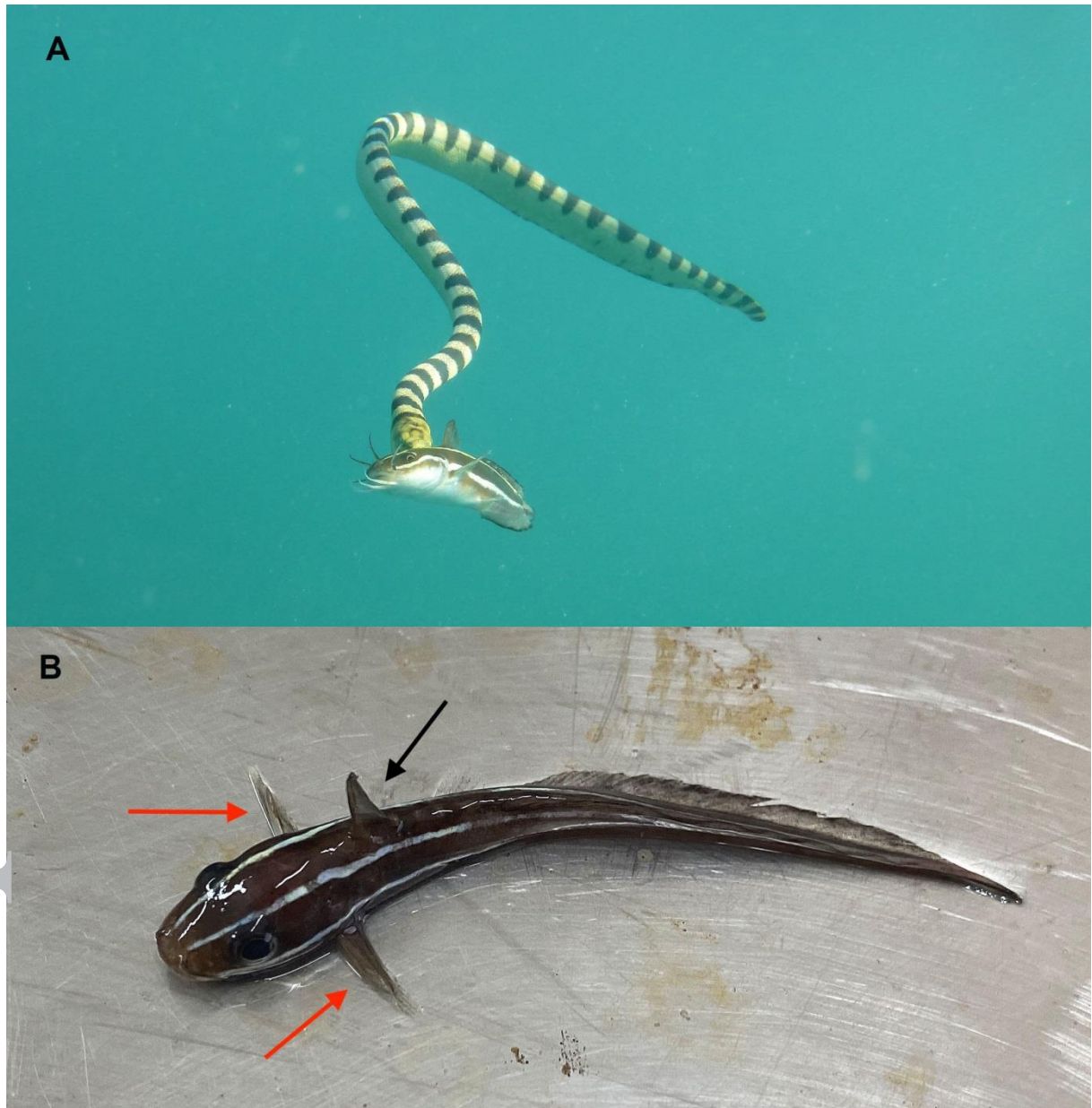


Figure 2. Effect of spine erection by Striped Eel Catfish (*Plotosus lineatus*) on the time taken for Greater Seasnakes (*Hydrophis major*) to (a) manipulate the prey after striking, and (b) to ingest the prey item.

Note that all prey-handling times are ln-transformed. Error bars show standard errors. The data are based on consumption of 12 catfish (6 with spines erect, 6 with spines folded down) by five Greater Seasnakes.

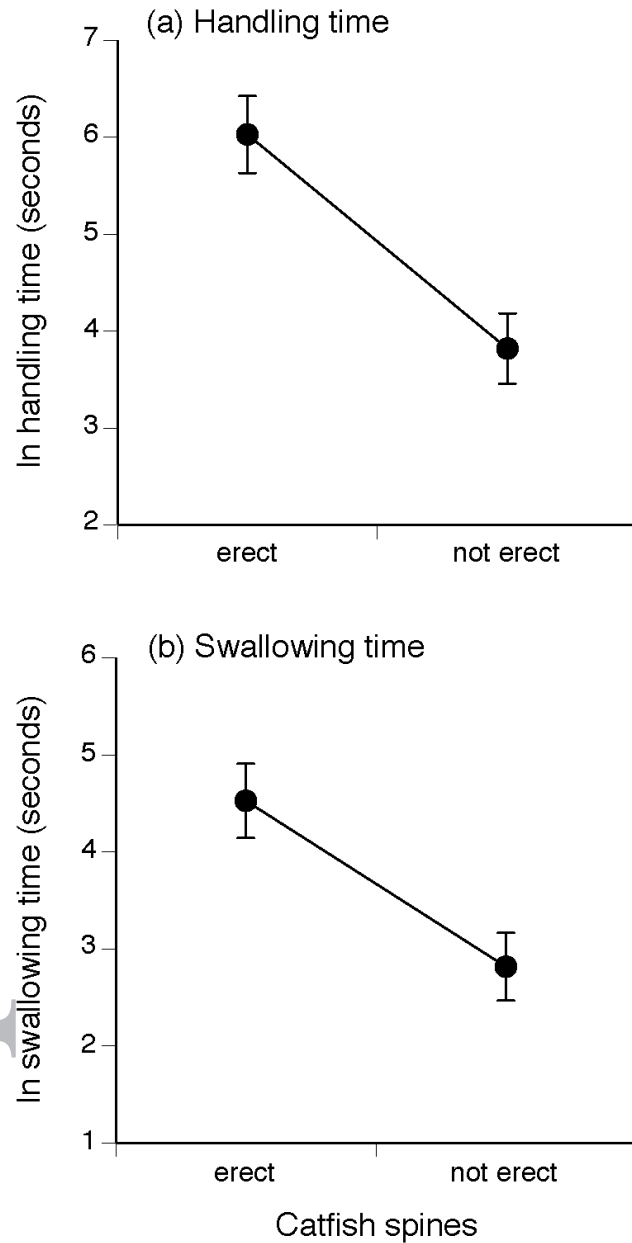


Figure 3. Geographic variation in the length of defensive spines in Striped Eel Catfish, *Plotosus lineatus*. The length of spines is calculated as the residual scores from the general linear regression of spine length (mean of pectoral and dorsal spines) against maximum body width (based on measurement of maximum horizontal and vertical dimensions of the trunk). Error bars shows standard errors. Some sites from which samples of catfish were available (left to right, on X-axis) but where Greater Sea Snakes do not occur were Lord Howe Island, (LH, N = 21), Asia (Indonesia, China, India, N = 10), New South Wales (NSW, N = 53), Madagascar (MG, N = 3), and Norfolk Island (NI, N = 20). Two other regions overlap partly but not completely with the snake's distribution (Queensland, QLD, N = 37; Papua New Guinea, PNG, N = 10). Finally, we measured spines in catfish from four sites where the species is sympatric with Greater Sea Snakes (tropical Western Australia, WA, N = 6; Northern Territory, NT, N = 15; Vanuatu, VU, N = 2; New Caledonia, NC, N = 21). In posthoc Tukey tests, mean spine lengths differed significantly between catfish from snake-sympatric *versus* snake-allopatric sites.

