



## Research

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**Author for correspondence:**

S. A. Price

e-mail: [saprice@ucdavis.edu](mailto:saprice@ucdavis.edu)

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# How predation shaped fish: the impact of fin spines on body form evolution across teleosts

S. A. Price, S. T. Friedman and P. C. Wainwright

Department of Evolution and Ecology, University of California Davis, 1 Shields Avenue, Davis, CA 95616, USA

It is well known that predators can induce morphological changes in some fish: individuals exposed to predation cues increase body depth and the length of spines. We hypothesize that these structures may evolve synergistically, as together, these traits will further enlarge the body dimensions of the fish that gape-limited predators must overcome. We therefore expect that the orientation of the spines will predict which body dimension increases in the presence of predators. Using phylogenetic comparative methods, we tested this prediction on the macroevolutionary scale across 347 teleost families, which display considerable variation in fin spines, body depth and width. Consistent with our predictions, we demonstrate that fin spines on the vertical plane (dorsal and anal fins) are associated with a deeper-bodied optimum. Lineages with spines on the horizontal plane (pectoral fins) are associated with a wider-bodied optimum. Optimal body dimensions across lineages without spines paralleling the body dimension match the allometric expectation. Additionally, lineages with longer spines have deeper and wider body dimensions. This evolutionary relationship between fin spines and body dimensions across teleosts reveals functional synergy between these two traits and a potential macroevolutionary signature of predation on the evolutionary dynamics of body shape.

## 1. Introduction

Linking ecological processes known to drive diversification on microevolutionary time scales to macroevolutionary patterns is one of the main challenges to understanding the evolution of phenotypic and lineage diversity. Species interactions are strong selective forces driving speciation and trait evolution as well as ecological dynamics. The impact of competition and predation writ large has been extensively investigated in the fossil record [1–4], but phylogenetic comparative studies of ecological interactions are more limited. The impact of competition on macroevolutionary patterns has generally been inferred phylogenetically by fitting diversity-dependent models (see review by Rabosky [5]) or through sister comparisons of disparity and range overlap [6,7], although recent developments provide explicit competition-based models of trait evolution [8,9]. The impact of predation has however been neglected by phylogenetic studies. Within prey species, predators are viewed by some as the single most important agent of change [10]. Predators can drive rapid adaptive changes in phenotypes [11,12], and many evolutionary models demonstrate how predation may drive morphological and species diversification (see reviews by [13,14]).

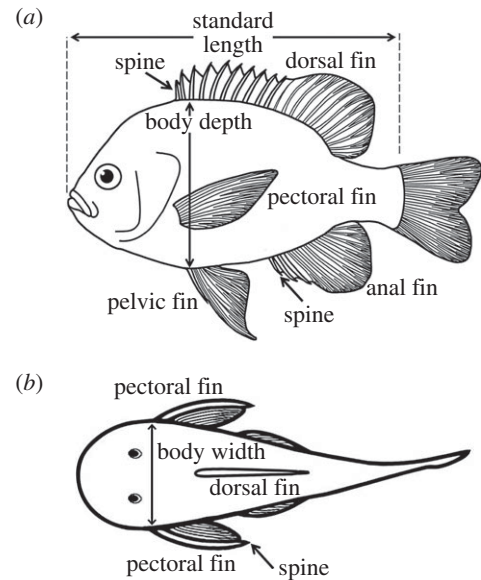
The impacts of predation on fish morphology, life history and behaviour are well studied experimentally and on a population level [11,15,16]. Morphologically, two changes are consistently identified in fishes exposed to different predation pressures. The first is (unsurprisingly) an increase in the number and size of defensive structures, such as fin spines and armour plates, when predation pressure is higher. Several fish lineages have evolved spines that are formed from modified fin rays within one or more of their fins (dorsal, anal, pectoral or pelvic fin). Spines act as a defence against predators [17] by deterring predation attempts [18], reducing capture success or making it difficult for the predator to ingest the

fish [19]. In wild fish populations, spine length increases with predator abundance [20,21] and predators have greater success eating individuals with shorter spines [22]. Moreover, a recent experiment found increases in length of the dorsal-fin spine relative to body length are induced in the presence of predators or predation signals [23].

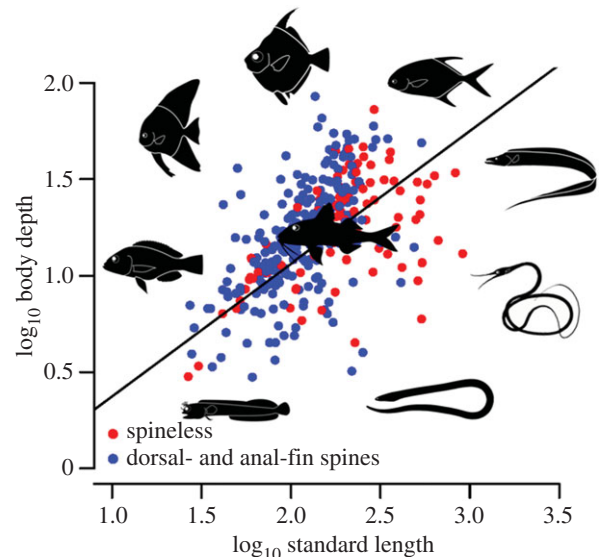
The second consistent change in the presence of predators is in body shape. Common garden experiments have shown that the presence of predators or predation cues induces an increase in the body depth-to-length ratio in the juveniles of a diversity of fishes, including crucian carp (*Carassius carassius* [11]), perch (*Perca fluviatilis* [24]), goldfish (*Carassius auratus* [25]), Nicaragua cichlids (*Hypsophrys nicaraguensis* [26]) and three-spined stickleback (*Gasterosteus aculeatus* [27]). Similarly, populations of fish experiencing higher predation have deeper bodies [28,29]. Being deeper bodied is a morphological defence against gape-limited predators [11,30] such as piscivorous fish and some fish-eating birds (e.g. herons, kingfishers and grebes). Even individuals that have not yet exceeded the predators gape may benefit by being deeper, as predators often prey more frequently on fishes well below the maximum size ingestible [31,32]. Moreover, handling time increases with prey body depth [21,30,33], increasing the likelihood of escape. Whether the link between predators and increased body depth is direct or indirect is still debated, as it may be the consequence of altered behaviour [34] such as reduced activity in the presence of predators [35] or differential habitat use and diet [36]. The effect of predator pressure on shape may even reflect a functional trade-off between foraging performance in different habitats and predator avoidance [37].

The hypothesis that predation promotes the diversification of fishes has a long history [38,39]. Although there is the potential for mismatches across scales, predictions from short-term local observations provide useful 'seeds for a macroevolutionary hypothesis' [40, p. 716]. Population-level genetic divergence along with adaptive plastic responses to predators can drive microevolutionary change, speciation and thus potentially macroevolutionary patterns [41,42]. To investigate the macroevolutionary signature of predation, we focus on the relationship between fin spines and body dimensions. Body shape may be influenced by numerous selective forces [43], but spines are primarily an anti-predator trait, though they may also aid locomotion and have been co-opted for communication in some lineages [44].

On microevolutionary time scales, predation influences both body shape and spine length, and experimental evidence also reveals that these two traits increase concomitantly in the presence of predators [23]. Although body depth has been the only body dimension to be studied experimentally, increases in body width may also be a morphological defence against gape-limited predators. Moreover, synergy between spines and body dimensions may be energetically the most cost-efficient way to exceed the gape limitations of predators. To be active anti-predator structures spines must not be easily broken or pressed against the body by the predator's jaws [45], and can be associated with additional defences such as venom [46]. However, spines of any length or robustness will increase the effective body size dimensions of the fish, potentially deterring gape-limited predators. If true, we would expect that the orientation of the spines predict which body dimension is the most likely to concomitantly increase in the presence of predators. Spines can be present on the dorsal, pectoral, anal and pelvic fins (figure 1).



**Figure 1.** (a) Lateral view diagram of a generalized acanthomorph fish illustrating the position of fins, spines and several linear morphometric measurements. (b) Dorsal view diagram of a generalized siluriform fish illustrating the position of the fins, spines and body width measurements.



**Figure 2.** The phylogenetic regression between  $\log_{10}$  standard length and  $\log_{10}$  body depth for families that have dorsal- and anal-fin spines (blue), and those that do not (red). Silhouettes illustrate some of the extremes of body shape, starting at the bottom left and going anti-clockwise: Chaenopsidae, Moringuidae, Nemichthyidae, Alepisauridae, Bramidae, Caproidae, Ehippididae and Cichlidae, with Mullidae in the center.

Fishes with fin spines projecting in the horizontal plane (pectoral-fin spines) should increase their body width, whereas those with spines on the vertical axis (dorsal-fin, anal-fin or pelvic-fin spines) should increase in body depth.

Across the teleost tree of life, there is a high degree of variability in body dimensions, as well as in the presence and length of fin spines (figure 2). We explore the influence that the three most common fin spines (dorsal, anal and pectoral) have on body depth and body width across teleost fishes, using phylogenetic comparative methods. Across teleosts, we expect dorsal- and anal-fin spines to have opened up a new and deeper body depth optimum, and pectoral-fin spines a new and wider body width optimum compared

with spineless lineages. Moreover, if spines and body dimensions are working together to reduce predation by gape-limited predators, we would also expect to find a positive relationship between spine length and body dimensions among species: lineages with longer spines on their dorsal and anal fins should be deeper bodied, whereas those with longer pectoral-fin spines should have wider bodies. In order to encompass the diversity of fin spines across teleosts, we focus on the family level, which will provide sufficient data for the analyses without requiring the measurement of thousands of species. Moreover, existing body shape data from several thousand acanthomorph species [47] suggests some of the most dramatic differences in relative body depth occur between families (see electronic supplementary material, table S1).

## 2. Methods

### (a) Phylogenetic data

We used the most comprehensive existing time-calibrated molecular phylogeny of fishes [48]. The phylogeny was built using maximum likelihood with branch lengths optimized using penalized likelihood [48]. We pruned the phylogeny to the family level by randomly sampling a single exemplar species for each family. Each species in the phylogeny was assigned to a family using the FishBase systematic classification, which was accessed via the `RFISHBASE` package v. 0.2.2 [49] in the R statistical computing framework [50]. To take into account the possibility of families being non-monophyletic, we randomly sampled an exemplar species per family 100 times and ran all analyses across the resulting topologies. Traditionally built but less comprehensive phylogenies of teleost clades show some different family-level relationships [51,52]; to see if this was likely to change our results we also ran additional analyses on an alternative, albeit smaller topology [51] (see electronic supplementary material, table S2).

### (b) Morphological data

Measurements were made on adults of one species from 347 teleost families in the research collection of P. C. Wainwright or the ichthyology collection at the California Academy of Sciences, thus including 77% of extant teleost families [53]. When there was a choice, each exemplar species was selected to be typical of the most common body form and spine configuration found across the family. We generated a morphological dataset of seven traits. These included three linear body dimension traits (standard body length, maximum body depth and maximum body width) along with the lengths of the anterior-most major spine in the dorsal fin, anal fin and pectoral fins (including both right and left fins; figure 2). For the purposes of this study, we made no distinction between unsegmented spines and the spines formed from a bundle of fused rays, as found in the dorsal fins of catfishes. All traits were measured in millimetres (mm) with hand-held dial callipers on one to three specimens per species, measuring three specimens when available. From these data, we generated two composite spine datasets; the first was the sum of the dorsal and anal-fin spine lengths, and the second the sum of the left and right pectoral spines lengths. These values were then  $\log_{10}$ -transformed.

### (c) Stochastic character mapping

To infer the history of spines through time we first converted the spine lengths to a presence/absence score (absent = 0 mm in length and present >0 mm in length) for pectoral-fin spines and dorsal-fin and anal-fin spines combined. We then used stochastic

character mapping [54,55], implemented in the R package `PHYTOOLS` [56], to estimate the histories of the two spine traits. Character histories were simulated by fixing the transition rate matrix ( $Q$ ) at the maximum-likelihood estimate, and the prior on the root state was estimated from the stationary distribution. We generated 50 character histories for each of the 100 family-level phylogenies; owing to computational constraints subsequent model-fitting analyses in `OUwie` (see below) were run on a random sample of 500 stochastically mapped trees.

### (d) Generalized Ornstein–Uhlenbeck models

We test our predictions using generalized Ornstein–Uhlenbeck (OU) models [57–59], which allow the presence and absence of spines to influence the primary optima of body depth or width ( $\theta$ ), the stochastically constant rate of depth or width evolution ( $\sigma^2$ ), and/or the strength of pull towards the primary optima ( $\alpha$ ).  $\theta$  is the trait value reached by an ‘infinite number of populations identical to the common ancestor evolving independently’ [57, p. 1342] with spines in a fixed state, and thus quite different from the realized trait optimum in real populations. The primary optima estimated across teleosts for spiny and spineless lineages allow us to gauge the influence of spines on fish body dimensions against a randomized evolutionary and ecological background. The strength of selection towards the primary optimum,  $\alpha$ , reflects the phylogenetic covariance between species and determines how quickly  $\theta$  will be reached following a state change. When  $\alpha$  is low, it indicates that the trait places weak constraints on body depth or width and that influence of phylogeny on the trait is high.  $\sigma^2$  is a constant, describing the rate of stochastic evolution around  $\theta$ . When  $\alpha = 0$ , the OU model collapses to a simple Brownian motion (BM) model. Under BM, all else being equal, higher  $\sigma^2$  indicates that there is greater disparity in body dimensions between closely related species [60] in the same state (i.e. with or without spines).  $\alpha$  and  $\sigma^2$  combined as  $\sigma^2/2\alpha$  determines the stationary variance of the joint OU–BM process [57]. This is a measure of the relative influence of stochastic factors, including unmeasured selective forces and phylogeny, in the adaptive process relative to the primary adaptive force. As we are looking broadly across teleosts and there are numerous factors that can influence body depth and width, we expect the estimates of  $\sigma^2/2\alpha$  to be high.

We used a model-fitting approach implemented in the R package `OUwie` [61] to compare seven different evolutionary models. As larger fish will have wider and deeper bodies on an absolute scale, we removed the influence of body size by analysing the residuals from a phylogenetic generalized least-squares (GLS) regression of  $\log_{10}$  width and  $\log_{10}$  depth against  $\log_{10}$  standard length [62], as implemented in the R package `PHYTOOLS` [56]. Therefore, positive estimates of  $\theta$  will indicate body dimensions greater than expected for their standard length, whereas estimates close to zero reveal that the optimal body dimension matches the allometric expectation. The first two models fit a single-rate (BM1) and a single-optima model (OU1) to the data, which allow body depth or width to evolve independently of spines. If either BM1 or OU1 are the best-fitting model, then there is no evidence that the presence or absence of spines influences the evolution of body depth or width across teleosts. The other five models allow one or more of the three OU parameters ( $\theta$ ,  $\sigma^2$ ,  $\alpha$ ) to vary depending on the presence or absence of spines. There is a two-rate model (BMS), a two-optima model (OUM), a combined two-optima model with separate estimates of the strength of pull towards those optima (OUMA) and a combined two-optima model with separate estimates of the rates of stochastic variance around them (OUMV). Lastly, the most complex model (OUMVA) allows  $\theta$ ,  $\sigma^2$  and  $\alpha$  to vary with respect to spines. The estimated primary optima from the OUM, OUMA, OUMV and OUMVA models indicate the influence that spines have on body depth and width. We



**Table 1.** Model fit as calculated by AICc weights for generalized OU models. Models are as follows: BM1, single-rate Brownian motion (BM) model; OU1, peak Ornstein–Uhlenbeck (OU) model; BMS, multi-rate Brownian model with different rates in spiny and spineless lineages; OUM, multi-peak OU model with different optima for spiny and spineless lineages but the same  $\alpha$  and  $\sigma^2$ ; OUMA, multi-peak OU with different optima and  $\alpha$  for spiny and spineless lineages but the same  $\sigma^2$ ; OUMV, multi-peak OU with different optima and  $\sigma^2$  for spiny and spineless lineages but the same  $\alpha$ ; OUMVA, multi-peak OU with different optima,  $\alpha$  and  $\sigma^2$  for spiny and spineless lineages.

body dimension	spines	BM1	OU1	BMS	OUM	OUMA	OUMV	OUMVA
depth	dorsal- and anal-fin spines	0.005	0.023	0.010	0.045	0.094	0.028	0.793
width	dorsal- and anal-fin spines	0.001	0.135	0.002	0.128	0.107	0.073	0.540
depth	pectoral-fin spines	0.063	0.422	0.026	0.153	0.064	0.076	0.200
width	pectoral-fin spines	0.000	0.000	0.000	0.003	0.012	0.035	0.950

predict that lineages with fin spines will have deeper/wider bodies plus greater variability in body dimensions; therefore, the best-fitting models should be OUMA, OUMV or OUMVA. These three models allow spiny and spineless lineages to have different primary optima and variance around them, either driven by  $\alpha$  (OUMA),  $\sigma^2$  (OUMV) or  $\sigma^2/2\alpha$  (OUMVA). As we have no expectations of a relationship between pectoral-fin spines and body depth or dorsal- and anal-fin spines and body width, we would predict that the BM1 or OU1 will be the best fit for these analyses.

We fitted the seven generalized OU models across 500 stochastically mapped trees of 347 teleost families. As our preliminary analyses indicated that the estimates of  $\theta$  for spiny and spineless lineages were stabilized by assuming  $\theta$  at the root was distributed according to the stationary distribution of the OU process, we set `root.station = TRUE` for all analyses. We checked the results of the OU<sub>WIE</sub> analyses to ensure that the eigenvalues of the Hessian were positive, as this is an indicator that the parameters were reliably estimated [58]. When a negative eigenvalue was found, we removed the results for that model and tree combination from the final dataset. Using the Akaike information criterion corrected for small sample size (AICc) [63], we calculated the relative strength of support for each model in the set using Akaike weights.

### (e) Phylogenetic generalized least-square regression

We estimated the relationship between body depth or body width and spine length using phylogenetic generalized least-squares (PGLS) regression on the 100 family-level phylogenies, implemented in the R package `CAPER` [64]. We took overall size differences into account by adding  $\log_{10}$  standard length as a covariate to every analysis. In addition, to account for the degree of phylogenetic covariation within the residuals of the model, we used the maximum-likelihood estimate of Pagel's  $\lambda$  [65] to transform the internal branches of the phylogeny.  $\lambda$  varies between 1, which indicates perfect phylogenetic signal as would be expected under a BM model, and 0, which indicates no phylogenetic signal. This transformation can be used to take into account non-Brownian-like patterns within the data that may be generated by a variety of evolutionary processes.

## 3. Results

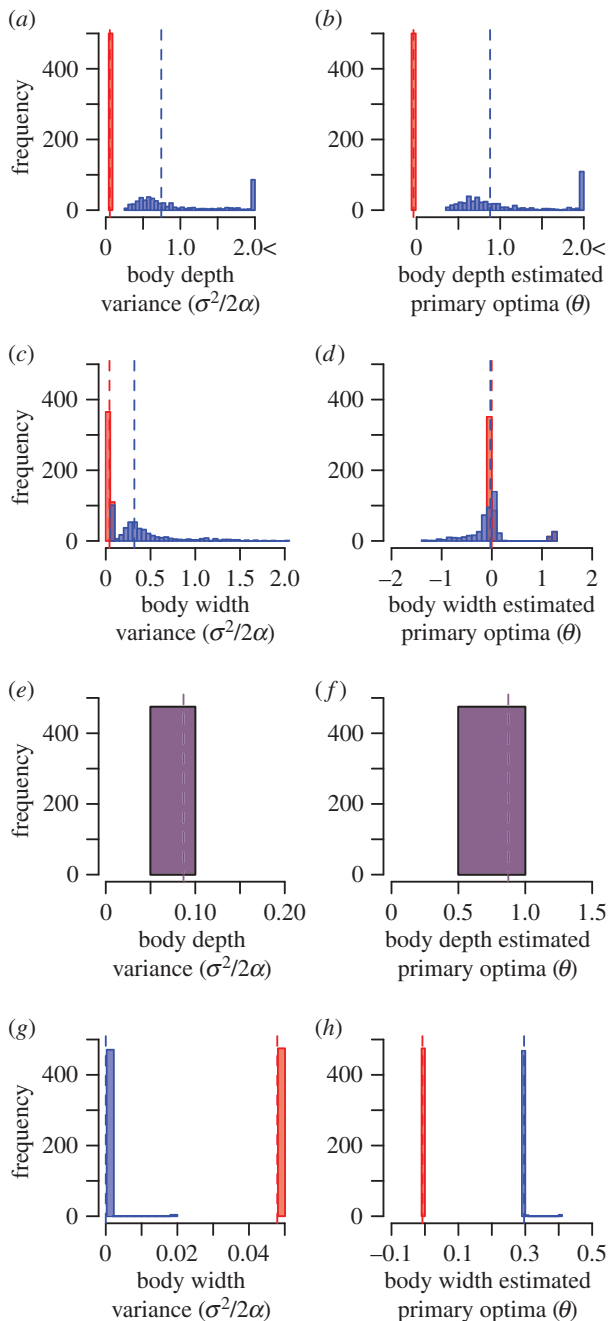
### (a) Stochastic character mapping

Dorsal-fin spines were found in 248 of the 347 teleost families sampled. Of those families with dorsal spines, 224 also had anal spines. We sampled no species that possessed an anal spine but no dorsal spine. Pectoral-fin spines were found in 28 siluriform (catfish) families and 21 of these also had

dorsal-fin spines. From the stochastic character maps, we inferred a history of gains and losses of spines across teleost fishes. At the family level, pectoral spines evolved just once and were lost a median of three times across the phylogeny, all within the Siluriformes (see electronic supplementary material, figure S1). Dorsal- and anal-fin spines show greater evolutionary lability, with a median of six independent gains of spines, several of which occurred within catfishes, and seven losses across teleosts (see electronic supplementary material, figure S2). Our phylogenetic sampling scheme underestimates the actual number of independent gains and losses of spines as the presence of spines can be variable within families. The two cases we are aware of are the Cyprinidae (the exemplar species we sampled lacked spines, but some species have evolved dorsal or anal-fin spines) and the Syngnathidae (which includes many species without fin spines, but the species we measured had very short dorsal spines).

### (b) Generalized Ornstein–Uhlenbeck models

The most complex model, OUMVA, is the best-fitting model for pectoral-fin spines and relative body width (AICc weight = 0.95) and for dorsal- and anal-fin spines and relative body depth (AICc weight = 0.793; table 1; electronic supplementary material, table S3). These results match our predictions as the best-fitting models allow both the primary optimum and the variance around it to vary depending on the presence or absence of spines. Moreover, when we look at the parameter estimates from the best-fitting models (figure 3), they also broadly fit our expectations. The primary optimum for relative body depth is positive for lineages with dorsal-fin and anal-fin spines (figure 3b), which means that the optimal body depth for spiny lineages is deeper than expected for their body size. In contrast, the primary optimum for spineless lineages is close to zero, indicating that they fit the allometric expectation. For relative body depth, the stationary variance of the OU process is greater within spiny lineages (figure 3a). This pattern may reflect that lineages without dorsal- and anal-fin spines are phylogenetically restricted, close to the base of the teleost tree, whereas spiny lineages encompass a wide diversity of teleost families. Similarly, the primary optimum for relative body width is positive in lineages with pectoral-fin spines, revealing that the optimal body width exceeds allometric expectations, while it is close to zero in lineages without pectoral-fin spines (figure 3h). For body width, lineages with pectoral-fin spines have lower variance around the primary optimum of body width



**Figure 3.** Histograms showing the distribution of the estimated optima ( $\theta$ ) and the variance around the optima ( $\sigma^2/2\alpha$ ) from the generalized Ornstein–Uhlenbeck models for spiny (blue) and spineless (red) lineages. Plots (a–d) are the results for lineages with dorsal and anal-fin spines, and (e–h) are the results for lineages with pectoral spines. The probability density was generated by running the analyses on 500 stochastically mapped trees, thereby representing the uncertainty in the result owing to non-monophyly of families and the mapping of spines upon the tree. The vertical lines represent the median for each category.

(figure 3g), which is perhaps not surprising as pectoral-fin spines are restricted phylogenetically to Siluriformes (catfishes).

As expected, if fin spines and body dimensions work synergistically to exceed the predators gape limitations, we see no effect of spines on the body dimension that does not parallel the orientation of the spine(s) (table 1 and figure 3). The best-fitting model for relative body depth and pectoral spines is a single optimum model (OU1, AICc weight = 0.422). Although the best-fitting model for relative body width and presence of dorsal- and anal-fin spines is the most complex model (OUMVA, AICc weight = 0.54), the distributions of the

estimated primary optima of body width are highly overlapping for spiny and spineless lineages (figure 2d). However, the variance around the width optimum is greater in lineages that have dorsal- and anal-fin spines (figure 3c).

The distribution of parameter estimates (figure 3) illustrates the influence of tree topology, which differ if there are non-monophyletic families, as well as the different character mappings of spines upon the phylogenies. The variance in the estimates reveal that topological and character history differences has a greater impact on the inference of the parameter estimates of lineages with dorsal- and anal-fin spines, as a few combinations of tree and character history lead to extremely large estimates of  $\theta$  and  $\sigma^2/2\alpha$ . For the purposes of illustration, we have combined all of the extreme estimates into the last column in the histogram in figure 3. The standard errors around the median parameter estimates (which include the approximate standard error of the model parameters as calculated from the Hessian matrix as well as the variance across the tree topologies and stochastic character maps) can be found in electronic supplementary material, table S4.

### (c) Phylogenetic generalized least-square regression

As predicted, there is a significant positive relationship between pectoral-fin spine length and body width, but not body depth, when standard length is added as a covariate (table 2). We also find a significant positive relationship between dorsal- and anal-fin spine length and both body depth and width, when standard length is included in the multivariate phylogenetic regression. The relationship between dorsal- and anal-fin spine length and body width remains even after catfishes with pectoral spines are removed (see electronic supplementary material, table S5). The 95% confidence intervals calculated from the PGLS analyses on the 100 family-level phylogenies reveal that non-monophyletic families have very little impact on the results. These results were not altered substantially by using the alternative phylogeny (electronic supplementary material, table S2).

## 4. Discussion

We have identified macroevolutionary relationships between fin spines and body form across teleost fishes that are consistent with the morphological changes driven by predators intraspecifically on microevolutionary time scales [23]. As predicted, if spines and body dimensions evolve synergistically to increase the minimum gape required to capture them, the orientation of the fin spines dictates which body dimension expands. Fin spines oriented on the vertical plane (dorsal and anal fins) open up a deeper body depth optimum, whereas spines on the horizontal plane (pectoral fins) open a wider body width optimum, both of which exceed allometric expectations. Spines, however, have no influence on the optimum of the opposing body dimension, and the optimum of spineless lineages matches the allometric expectation for both depth and width. Further support for spines and body dimensions evolving together is provided by the result that even after body size is accounted for, spine length and relative body dimensions are significantly and positively related.

The possibility that developmental or pleiotropic linkages are driving the relationships we observe between spines and body dimensions cannot be ruled out. Unfortunately, little is known about the developmental control of these traits.

**Table 2.** Phylogenetic regression table showing relationship between spine length and body dimensions.

body measure	spines	estimate (95% CI)	s.e. (95% CI)	t-value (95% CI)	p-value (95% CI)	adjusted $r^2$ (95% CI)	estimated lambda (95% CI)
$\log_{10}$ depth	$\log_{10}$ dorsal- and anal-fin spine length	0.147 (0.126–0.154)	0.147 (0.146–0.148)	0.996 (0.857–1.043)	0.320 (0.300–0.392)	0.407 (0.397–0.411)	0.865 (0.713–0.976)
	(intercept)	0.223 (0.210–0.226)	0.030 (0.029–0.030)	7.557 (7.197–7.646)	$3.77 \times 10^{-13}$		
$\log_{10}$ width	$\log_{10}$ standard (body) length	0.582 (0.579–0.592)	0.050 (0.050–0.050)	11.681 (11.602–11.879)	0 (0–0)		
	(intercept)	–0.223 (–0.234 to –0.216)	0.132 (0.131–0.133)	–1.688 (–1.770 to –1.639)	0.092 (0.078–0.102)	0.426 (0.422–0.430)	0.801 (0.618–0.921)
$\log_{10}$ depth	$\log_{10}$ dorsal- and anal-fin spine length	0.149 (0.142–0.151)	0.027 (0.026–0.027)	5.510 (5.405–5.574)	$7.06 \times 10^{-8}$		
	(body) length	0.634 (0.631–0.639)	0.046 (0.046–0.046)	13.733 (13.637–13.911)	$5.05 \times 10^{-8}$		
$\log_{10}$ width	$\log_{10}$ standard (body) length	0.038 (0.030–0.047)	0.159 (0.158–0.159)	0.241 (0.190–0.297)	0.810 (0.767–0.849)	0.313 (0.309–0.317)	0.875 (0.694–0.995)
	(intercept)	0.064 (0.062–0.065)	0.046 (0.045–0.046)	1.403 (1.369–1.427)	0.162 (0.155–0.172)		
$\log_{10}$ depth	$\log_{10}$ pectoral-fin spine length	0.650 (0.650–0.650)	0.053 (0.053–0.053)	12.258 (12.152–12.347)	0 (0–0)		
	(body) length	–0.274 (–0.281 to –0.269)	0.137 (0.136–0.137)	–2.005 (–2.065 to –1.973)	0.046 (0.040–0.049)	0.386 (0.382–0.390)	0.803 (0.581–0.937)
$\log_{10}$ width	$\log_{10}$ pectoral-fin spine length	0.098 (0.097–0.100)	0.040 (0.040–0.040)	2.439 (2.40–2.482)	0.015 (0.014–0.017)		
	(body) length	0.669 (0.667–0.672)	0.047 (0.047–0.047)	14.146 (14.055–14.276)	0 (0–0)		

Within three-spined stickleback using the marine and benthic lake form, it has been inferred that bony plates, pelvic-fin spines and body depth may be linked [66]. However, in the wild these lineages show the opposite pattern to the one we identify across teleosts: benthic forms, which are deeper bodied, have reduced armour. The explanation for this pattern within sticklebacks is differential predation between habitats. In the benthic habitat, insects are the primary predator, and this is thought to drive the loss of spines, as the spines can be used by the insect larvae to grab hold of the fish [67], whereas in marine and limnetic habitats, gape-limited predators reign.

Across teleosts we inferred a single origin of pectoral-fin spines, probably at the base of Siluriformes (posterior probability 0.72), which means there is no evolutionarily independent replication to confirm that fishes with these spines have wider bodies. It is therefore possible that a co-distributed factor could be driving the association between body width and pectoral spines. For example, catfishes are frequently benthic, and bottom-dwelling fishes are often dorsoventrally flattened [68]. Among other consequences, this shape may allow fishes to enhance contact with the substrate when they are at rest. However, the significant positive relationship between pectoral spine length and body width appears to provide strong support for the hypothesis that pectoral spines and body width are evolving in tandem. While the strong contrast between catfishes and the lineages that do not have pectoral spines could potentially be biasing the estimated relationship between width and spine length, a significant positive relationship remains when only catfish families with pectoral-fin spines are analysed (see electronic supplementary material, table S6). We therefore conclude that pectoral-fin spines do influence body width in the expected direction. The additional selective advantages conferred on wide-bodied benthic catfishes may explain the lower variance in body width across lineages with pectoral spines estimated from the OU models.

Dorsal- and anal-fin spines are common across the teleost tree, evolving a median of six times at the family level in our analyses. Across teleosts, we recover the expected relationship between the presence and absence of dorsal and anal-fin spines and body depth, with the primary optima for spiny lineages being deeper and with greater variance around the optima than spineless lineages. We find no influence of dorsal- and anal-fin spines on the estimated primary optima of relative body width, which fits our predictions, because the spines are oriented on a different axis to the body dimension. However, the best-fitting model is still one that estimates separate  $\alpha$ ,  $\sigma^2$  and  $\theta$  for body width in spiny and spineless lineages, with the variance around the optima ( $\sigma^2/2\alpha$ ) being much higher in lineages with dorsal- and anal-fin spines. This result is driven by the catfishes, which have greater relative body widths than most teleosts along with pectoral spines: when we re-run the analyses removing the lineages with pectoral spines, the best-fitting model is OU1 (see electronic supplementary material, table S7). Interestingly, the significant positive relationship between dorsal- and anal-fin spine length and relative body width is not similarly explained by the inclusion of catfishes, as the relationship persists after their removal (see electronic supplementary material, table S4). Diversity of body shape, along both the dorsal-ventral and lateral axes, is enhanced in lineages with spines in the dorsal and anal fins.

There are 92 families for which the exemplar species we measured had no dorsal-, anal- or pectoral-fin spines. Most spineless families are towards the base of the teleost phylogeny, primarily in Osteoglossomorpha and Elopomorpha (the notable exception being the spiny eels: Notacanthidae), along with basal Ostariophysi and Euteleostomorpha families, which includes salmon and trout. We expect that spineless lineages or families with much shorter spines than expected for their size should have alternative anti-predator strategies. For example, the electric catfishes (Malapteruridae) lack fin spines, and the one spineless acanthomorph family in our dataset (Synbranchidae) burrow in mud and thick vegetation. Within spiny lineages, there are seven very slender-bodied families, including the Notacanthidae, which are extreme outliers with much shorter spines than expected for their body depth (see electronic supplementary material, figure S3). Many of these families exhibit behaviours such as burrowing (Ammodytidae, Mastacembelidae, Ptilichthyidae), living as commensals within invertebrates (Carapidae), hiding using camouflage (Sygnathidae) or live in habitats like the deep sea (Notacanthidae), which may provide anti-predator benefits and sometimes even select against spines.

Our findings and predictions concerning the synergy between fin spines and body dimensions theoretically spans evolutionary scales. If true, in response to predators species that have spines in their dorsal or anal fins will increase body depth, whereas species with pectoral spines ought to become wider, and those without spines may increase either dimension or exhibit alternative anti-predator strategies. Currently, every intraspecific experiment that demonstrates an increase in relative body depth in response to predation cues uses species with dorsal- and anal-fin spines [11,23–26]. Therefore, intraspecific experiments on adaptive plastic responses to predators in spineless species and catfishes with pectoral-fin spines are needed. Individually, spines and increases in body dimensions are a useful tool against predators, but together they may be more powerful.

The phylogenetic regression models reveal that body length and spine length combined only account for approximately 40% of the variance in body depth and width, which is noteworthy as allometric relationships between length and other size measurements across fishes are usually very tight (e.g. [69]). This result reflects the complex nature of body shape evolution, with interactions between ecological, social and functional factors ultimately determining the shape of fishes. For example, intraspecific studies have revealed an additive interaction between diet- and predator-induced morphological changes. The deepest individuals are those reared on benthic prey in the presence of predators, and the most slender are those reared on zooplankton in the absence of predation cues [70]. Therefore, the costs and benefits of deep and slender phenotypes depend on different ecological factors, such as predation risk versus competition [70]. Thus, only by including a wide variety of factors (such as habitat, trophic group, prey capture mode and mode of locomotion) into our macroevolutionary studies will we start to fully understand the remarkable diversity of body shapes that have evolved across the teleost tree of life.

**Ethics.** No human or animal subjects were used in this analysis, only museum specimens.

**Data accessibility.** All datasets are presented as electronic supplementary material.



**Authors' contributions.** S.A.P. designed and carried out the analyses and wrote the manuscript; P.C.W. conceived of the study, coordinated the study and helped draft the manuscript; S.T.F. collected the data, drew illustrations and helped draft the manuscript. All authors gave final approval for publication.

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