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ORIGINAL RESEARCH

Behavioral novelties and morphological exaptation underlie trophic novelty in an anemone-feeding fish

J. M. Huie[1], S. D. Arnette[2], A. J. Evans[1], K. E. Cohen[3], T. J. Buser[4], C. H. Crawford[5], E. A. Kane[6] & M. A. Kolmann[2]

[1]Biological Sciences, The George Washington University, Washington, DC, USA
[2]Department of Biology, University of Louisville, Louisville, KY, USA
[3]Friday Harbor Laboratories, University of Washington, Friday Harbor, WA, USA
[4]Department of BioSciences, Rice University, Houston, TX, USA
[5]Department of Biology, Coastal Carolina University, Conway, SC, USA
[6]Department of Biology, University of Louisiana at Lafayette, Lafayette, LA, USA

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Correspondence
Jonathan M. Huie, Biological Sciences, The George Washington University, 800 22nd St NW Suite 6000, Washington, DC 20052, USA.
Email: jonathanmhuie@gmail.com

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Abstract

Anemones are prominent members of marine ecosystems; however, of the 15 000 species of marine fishes, only 13 are documented to feed substantially on anemones. Preying on anemones may require specialized phenotypes to overcome their nematocyst-lined tentacles and elastic material properties. Here, we investigated whether *Clinocottus globiceps*, one of the few anemone-feeding fishes, has behavioral and morphological adaptations for consuming anemones. We used high-speed videography to describe the behaviors of *C. globiceps* and syntopic sculpins feeding on anemones and shrimp. We then compared the feeding apparatus of five trophically diverse sculpins using micro-computed tomography and scanning electron microscopy. We also used histology to investigate potential defense mechanisms for resisting nematocysts. We found that *C. globiceps* used a distinct combination of twisting and bending to rip anemone tentacles, compared to just the pulling or just rolling behaviors used by all species to feed on shrimp. Both *C. globiceps* and its algivorous sister species, *C. recalvus*, had robust jaws, large jaw muscles, and rows of blade-like teeth suited for biting that contrasted with the suction-feeding morphology of benthic invertivores. *Clinocottus globiceps* also had thicker epithelia around the mouth, which may act as a shield against nematocysts. We propose that the morphologies of *C. globiceps* that aid in anemone-feeding are likely exapted from algivory. We also emphasize the important role of behavior in facilitating trophic novelty.

Introduction

Morphological adaptation of the feeding apparatus often accompanies trophic evolution and may be required to access novel dietary niches (Freeman, 1979; Grant & Grant, 2002; Huertas & Bellwood, 2018, 2020; Hulsey & León, 2005; Martin & Wainwright, 2011; Rico-Guevara et al., 2019; Santana & Cheung, 2016). In an ecomorphological framework, it is often assumed that the feeding morphologies of predators match the physical characteristics of the prey (Ferry-Graham et al., 2002; Higham et al., 2021; Wainwright & Richard, 1995). Thus, morphological innovation may underlie access to new trophic niches (Hulsey, 2005; Konow et al., 2017; Price et al., 2010; Troyer et al., 2024). Alternatively, trophic transitions could be facilitated by preadapted traits that are co-opted (or exapted) for new resources (Davies et al., 2020). However, predators can modulate their feeding behaviors to increase feeding performance on different prey (Ferry-Graham et al., 2001; Kane, Cohen, et al., 2019; Kane, Roeder, et al., 2019; Nemeth, 1997), suggesting that changes in behavior alone could be sufficient to access new resources.

Fishes demonstrate a wide range of diets and feeding strategies that make them an ideal system for studying the evolution of trophic morphologies. Classic dietary guilds (i.e., herbivory, piscivory, and durophagy) exemplify how the mechanical properties of prey items promote strong form-function relationships. For example, durophagous fishes tend to have stout jaw bones and robust muscles for crushing hard-shelled prey, while piscivorous fishes tend to have long, protrusible jaws for capturing elusive prey (Cohen et al., 2020; Collar et al., 2009;

Huber et al., 2008; Mihalitsis & Bellwood, 2019; Rutledge et al., 2019; Turingan & Wainwright, 1993). Beyond these common guilds, many fishes also employ rare trophic strategies, such as feeding on the scales of other fishes (lepidophagy), parasites (cleaners), or coral polyps (corallivory) (Baliga & Mehta, 2018; Huertas & Bellwood, 2018; Huie et al., 2020; Kolmann et al., 2018). These trophic strategies may be rare, not because of prey scarcity, but because specialized phenotypes are required to access them (Martin & Wainwright, 2011, 2013). For example, the extraoral teeth and ramming behavior of scale-feeding characids are specialized compared to their relatives (Kolmann et al., 2018; Sazima, 1984). We therefore ask, to what extent does feeding on specialized prey require specialized phenotypes?

Sea anemones are sessile marine invertebrates found around the globe yet are infrequently preyed on by fishes (Ates, 1989; Fautin et al., 2013). There are approximately 15 000 species of marine fishes, but only 13 species from eight families are considered significant anemone predators (Ates, 1989; Carrete Vega & Wiens, 2012). The discrepancy between anemone availability and predator numbers suggests that anemones are challenging to feed on. A significant barrier to anemone predation, and cnidarians more broadly, are the toxic stinging cells (nematocysts) lining cnidarian tentacles (Kass-Simon & Scappaticci Jr., 2002). Fishes often tear off pieces of the tentacles rather than consuming the whole animal (Ates, 1989; Porat & Chadwick-Furman, 2004; Yoshiyama, Knowlton, et al., 1996; Yoshiyama, Wallace, et al., 1996). Tearing can be difficult because the elastic tissue comprising the anemone body wall (mesoglea) is resistant to shear and tensile stress (Koehl, 1977), and anemones can rapidly retract their tentacles (Shick, 1991). Investigating the morphological and behavioral traits of anemone-feeding fishes will provide insights as to how anemone predators overcome these challenges.

Anemone-feeding fishes likely have chemical and mechanical defenses for mitigating the effects of nematocysts. High densities of mucus-secreting goblet cells can prevent nematocysts from discharging (Greenwood et al., 2004; Huertas & Bellwood, 2017, 2018; Martin et al., 2007). Meanwhile, impenetrable tissues due to thickening or calcification of contact surfaces may serve as structural shields to inhibit impalement (Huertas & Bellwood, 2017, 2018; Martin et al., 2007). Additionally, anemone feeders may exhibit a reduction of sensory cells (e.g., taste buds) and vulnerable tissues in and around their mouths.

Mosshead sculpins (*Clinocottus globiceps*) are one of the few prominent anemone-feeding fishes (Ates, 1989). They are found in the rocky intertidal of the eastern Pacific Ocean, where sea anemones can make up ~66% of their diet (Grossman, 1986). In laboratory settings, *C. globiceps* feeds vigorously on anemone tentacles (Augustine & Muller-Parker, 1998; Brezina, 1979; Yoshiyama, Knowlton, et al., 1996; Yoshiyama, Wallace, et al. 1996). Yoshiyama, Wallace, et al. (1996) recounted that *C. globiceps* used “pronounced wrenching and tearing actions that involved the fish’s entire body” to feed on anemones. That suggests the use of a novel feeding mode distinct from rotational feeding used by some intertidal sculpins and elongate fishes to tear pieces from larger food masses (Crawford et al., 2025; Yoshiyama, Wallace, et al., 1996). *Clinocottus globiceps* also appear to be relatively unaffected by the nematocysts of their prey, including *Anthopleura elegantissima* that have deterring toxins capable of paralyzing shore crabs (Bruhn, et al., 2001; Yoshiyama, Wallace, et al., 1996).

In this study, we investigated the feeding behavior and morphology of *C. globiceps* to identify traits that facilitate anemone feeding. *Clinocottus globiceps* is unusual because most intertidal sculpin species are trophically conserved, feeding primarily on arthropods (Buser et al., 2019). *Clinocottus globiceps* can be found in the same tidepools with closely related, non-anemone-feeding sculpin species, supporting our prediction that anemone-feeding requires adaptive phenotypes. We used high-speed videography to record feeding behaviors of the syntopic *C. globiceps*, *C. embryum*, and *Oligocottus maculosus*, and a suite of bio-imaging techniques to compare the feeding apparatus of *C. globiceps* with those of closely related species. Our objectives were threefold: (1) describe behaviors used by sculpins to feed on anemones versus shrimp, (2) assess whether *C. globiceps* has a unique jaw morphology for tearing anemones compared to other sculpins, and (3) explore whether *C. globiceps* has distinct mechanisms for resisting nematocysts. We predict that *C. globiceps* exhibits traits that could facilitate anemone feeding, such as novel feeding behaviors, higher jaw mechanical advantage, larger jaw muscles, cutting dentition, more mucus cells, and thicker oral epithelium. Our work provides insight into how interactions between behavior and morphology facilitate access to novel dietary niches.

Materials and methods

Specimen acquisition

For feeding experiments, we collected wild *C. globiceps* (*n* = 8, 15.5–47.7 mm SL), *C. embryum* (*n* = 2, 40.1–48.0 mm SL), and *O. maculosus* (*n* = 5, 39.7–57.8 mm SL) (Table 1). Specimens of *C. globiceps* and *O. maculosus* were collected with handnets from tide pools at Cattle Point on San Juan Island, WA, while *C. globiceps* and *C. embryum* were collected from Iceberg Point on Lopez Island, WA. All animals were housed in a flow-through tank system at Friday Harbor Laboratories (FHL). We also collected *A. elegantissima* (*n* = 10, 25–40 mm in diameter) from Cattle Point and FHL and transplanted them onto ceramic tiles for feeding trials. After feeding experiments, fish were euthanized with tricaine-methanesulfonate (MS-222), fixed in 10% formalin, and stored in 70% ethanol. All procedures were approved by the University of Washington’s Institutional Animal Care and Use Committee (IACUC #4238-03).

To identify potential morphological adaptations for anemone-feeding, we compared preserved specimens of *C. globiceps, C. embryum*, and *O. maculosus* with two other closely related species: *Clinocottus recalvus* and *Orthonopias triacis* (Fig. 1). Preserved specimens were obtained through the FHL Fish Collection, Oregon State Ichthyology Collection (OSU), or the Scripps Institution of Oceanography Marine Vertebrate Collection (SIO) (Table S1).

Table 1 The sample size and standard length (mm) of the studied species by method

Species	Feeding trials	CT scans	diceCT	SEM	Histology
Clincottus globiceps	8 (15.5–47.7)	17 (15.5–116.1)	1 (34.6)	1 (33.6)	1 (27.7)
Clinocottus recalvus	—	13 (27.7–87.1)	1 (38.9)	1 (39.9)	1 (27.7)
Clinocottus embryum	2 (40.1–48.0)	10 (18.8–60.4)	1 (37.2)	1 (39.3)	1 (27.1)
Orthonopias triacis	—	11 (25.3–70.2)	1 (41.5)	1 (45.1)	1 (25.3)
Oligocottus maculosus	5 (39.7–57.8)	11 (18.6–71.1)	1 (34.5)	1 (37.7)	1 (26.4)

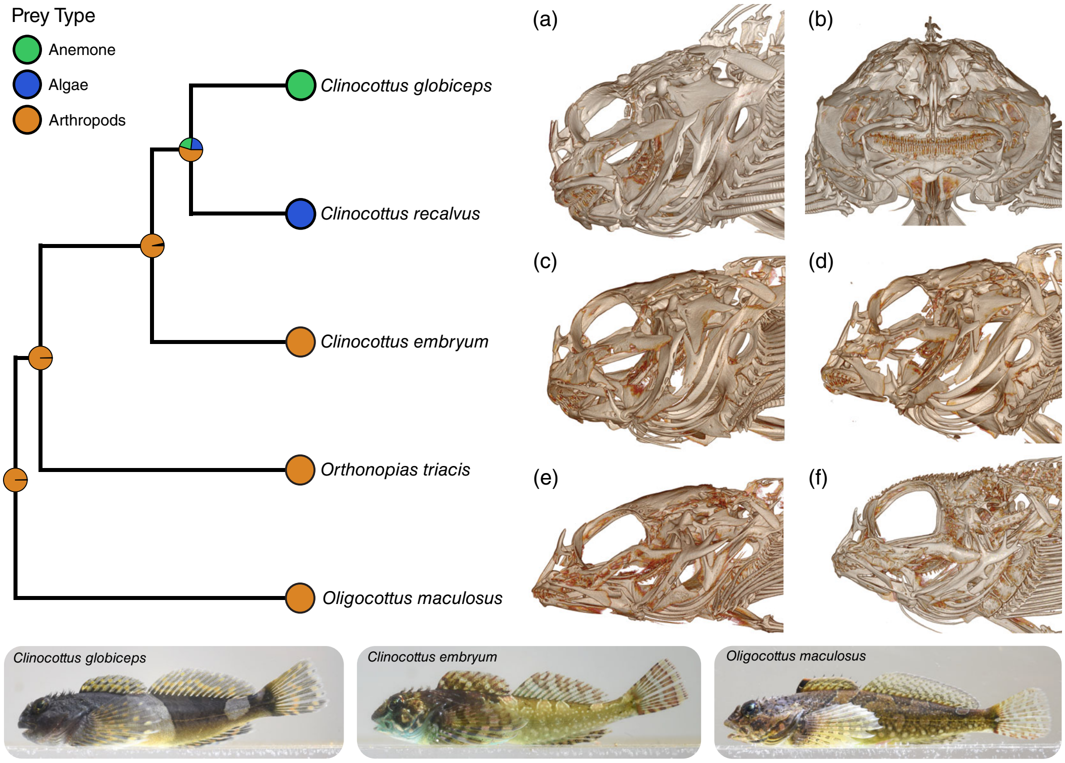

Figure 1 Phylogenetic relationships of the five sculpin species sampled in this study based on Buser et al. (2017) and an ancestral state reconstruction of diet. Morphological variation in skull shape is visualized using micro-CT scans. Lateral views of (a) *Clinocottus globiceps*, (c) *Clinocottus recalvus*, (d) *Clinocottus embryum*, (e) *Oligocottus maculosus*, and (f) *Orthonopias triacis*. (b) Anterior view of *C. globiceps*. Whole animal photos depict *C. globiceps*, *C. embryum*, and *O. maculosus*, which can be found together in the same tidepools and were studied in feeding trials.

Diet categorization and reconstruction

We reviewed published diet data and categorized the primary diet of each species based on reported frequencies and volumes. In addition to anemones, *Clinocottus globiceps* feeds substantially on algae (Grossman, 1986; Miller et al., 1980; Norton, 1995). Similarly, *Clinocottus recalvus* feeds primarily on algae (Johnston, 1954). The remaining species feed on various arthropods. *Clinocottus embryum* feeds on barnacle cirri, gammarid amphipods, and harpacticoid copepods (Miller et al., 1980; Simenstad & Nakatani, 1977). *Oligocottus maculosus* feeds on gammarid amphipods and harpacticoid copepods (Miller et al., 1980; Norton, 1995). *Orthonopias triacis* feeds on gammarid amphipods, decapod crab larvae, and polychaete worms (Burge & Schultz, 1973; Norton, 1995; Snook, 1997).

We performed an ancestral state reconstruction of diet to assess the evolutionary history of anemone feeding. We pruned the sculpin phylogeny from Buser et al. (2017) to include only our focal taxa and conducted a stochastic character mapping with 1000 simulations using the *phytools* R package version 2.4 (Bollback, 2006; Revell, 2024). We coded *C. globiceps* as an anemone feeder, *C. recalvus* as an algivore, and the remaining species as arthropod invertivores. Based on AIC scores, an equal-rates transition rate model was determined to be a better fit and was used instead of a symmetrical rates model or all-rates-different model. To account for uncertainty in trophic classifications, we performed a second analysis using a modified version of the synthetic diet categories from Buser et al. (2019). In this analysis, we coded *C. globiceps* and *C. embryum* as consumers of "tentacle and appendages," *C. recalvus* as a "stationary benthic item" feeder, and *O. maculosus* and *O. triacis* as "benthic arthropod" invertivores. In Buser et al. (2019), *C. globiceps* was coded as a "stationary benthic item" feeder because they did not consider anemones as a substantial dietary component. All analyses were performed in R version 4.3.2 (R Core Team, 2023).

Feeding behavior

We used high-speed videography to record the anemone-feeding behavior *C. globiceps* specimens (Table 1). *Clinocottus embryum* and *O. maculosus* were provided the opportunity to feed on anemones, but neither made attempts. Individual feeding strikes were filmed at 700 frames per second from the dorsal and lateral perspectives simultaneously, using two Edgertronic SC1 cameras (Sanstreak Corp., Campbell, CA, USA). We filmed in a 21 × 16 cm filming arena within a 5-gallon aquarium filled with natural seawater and illuminated with two LED flood lights. Prior to filming, a single fish and anemone were acclimated in the arena with dimmed lighting, separated by a temporary barrier for a few minutes to a few hours. During filming sessions, lighting was increased, and the barrier was removed to allow the fish to feed freely on the anemone. We recorded multiple feeding events per session and continued until the fish stopped feeding. The same anemones were used for consecutive feeding events and between sessions until they no longer extended their tentacles. To investigate the impact of prey type on feeding behavior and compare behaviors between species, we also recorded *C. globiceps* ($n = 1$, 37.3 mm SL), *C. embryum* ($n = 2$), and *O. maculosus* ($n = 5$) feeding on large pieces of fresh shrimp held with forceps. Water temperature (12–15°C) and oxygen levels were maintained through frequent water changes between sessions. All fishes were fasted for at least 3 days prior to and between feeding experiments.

Following a precursory inspection of the videos, we categorized feeding strikes into discrete feeding modes (see 'Results' section). Despite recording with two cameras, we could not reliably quantify the three-dimensional variation and opted for qualitative comparisons. We also attempted to confirm whether *C. globiceps* was successful by inspecting videos for evidence of damage to the anemones.

Feeding functional morphology

We used micro-computed tomography (μCT) scans to visualize and compare the cranial anatomy of five sculpin species. We sampled 10–17 specimens per species across a range of body sizes that included the size range of fishes used for feeding trials (Table 1). We generated new scans at the FHL Karel F. Liem Bio-imaging center using a Bruker Skyscan 1173 and downloaded existing scans on MorphoSource.org (Blackburn et al., 2024; Boyer et al., 2016; Buser et al., 2023). Scans were conducted at 65 kV, 123 μA, 1100–1170 s exposure time, and a voxel size between 8.1 and 26.9 μm. One specimen per species (Table 1) was scanned with contrast-enhancing stain to visualize jaw musculature following diceCT procedures described by Kolmann et al. (2023). Specimens were soaked in a 3.25% Lugol's Iodine solution for 32 h and scanned with similar scanner settings as the bone scans.

To investigate whether *C. globiceps* possess feeding morphologies that could facilitate anemone-feeding, we measured nine functional traits (Buser et al., 2019) (Fig. 2). These traits included anterior and posterior jaw closing mechanical advantage (the extent to which the lower jaw is modified for rapid or forceful closure), quadrate offset (the extent to which jaws close in a slicing or crushing manner), tooth aspect ratio (tooth shape and robustness), lower symphyseal height (jaw robustness), ascending process length (jaw protrusibility), premaxilla length (gape size), and the length and width of the lower jaw (gape size). Using the diceCT scans, we measured the volume of the A1, A2, and A3 subdivisions of the adductor mandibulae, the primary jaw-closing muscle in fishes. Measurements were collected using a modified procedure described in Buser et al. (2020) with the program 3D Slicer and the SlicerMorph toolkit (Kikinis et al., 2014; Rolfe et al., 2021).

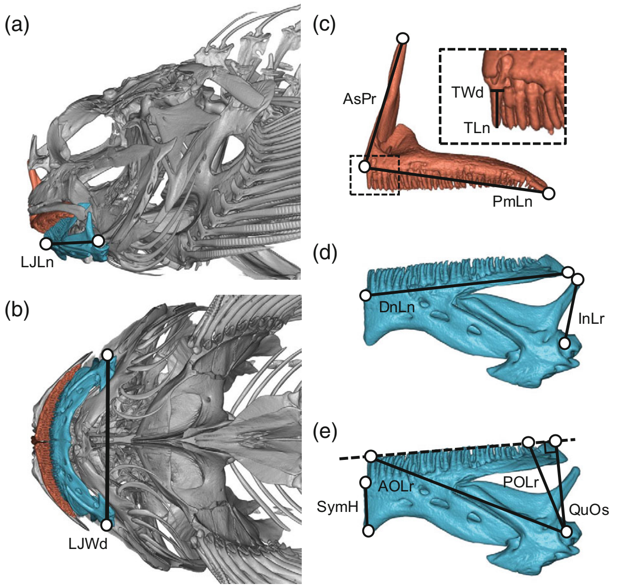

Figure 2 Morphological measurements used to compare the functional morphology of the feeding apparatus. Shown are (a) lateral and (b) ventral views of the head with the premaxilla (red) and lower jaws (blue) colored, (c) magnified view of the premaxilla, and (d, e) magnified views of the lower jaw. Measurement abbreviations are defined as follows: lower jaw length (LJLn), lower jaw width (LJWd), ascending process length (AsPr), premaxilla length (PmLn), tooth width (TWd) and height (TLn), dentary length (DnLn), mechanical advantage in-lever length (InLr), anterior mechanical advantage out-lever length (AOLr), posterior mechanical advantage length (POLr), symphyseal height (SymH), and quadrate offset (QuOs).

Intra- and interspecific variations in feeding mechanics were visualized using a phylomorphospace. All traits were log-transformed, and linear measurements were regressed against standard length. The residuals of the regressions were used as size-corrected trait values. Mechanical advantage, quadrate offset, and tooth aspect ratios were all already size-independent ratios. The nine functional traits were used to perform a principal component analysis that included intraspecific variation with a correlation matrix.

Scanning electron microscopy

We used scanning electron microscopy (SEM) to visualize tooth shapes at higher resolution. The lower jaw of one fixed specimen per species (Table 1) was removed, sonicated for 2 min, and dehydrated using an ethanol series. The samples were dried using a critical point dryer (Samdri 790, Tousimis Research Corp., Rockville, MD, USA) and sputter coated with gold palladium using a Cressington 108 Sputter Coater (Ted Pella, Inc, Redding, CA, USA). Samples were imaged with a JEOL Neoscope JCM-5000 (JEOL Ltd., Tokyo, Japan) and a Zeiss Evo 10 (Carl Zeiss AG, Oberkochen, Baden-Württemberg, Germany).

Histological sectioning

We used histological sectioning to assess the distribution of mucus cells and the thickness of the epithelium on the surface of the head, lips, and mouth in the five sculpin species. The head of one formalin-fixed specimen per species (Table 1) was removed from the body and bisected parasagittally. All samples were decalcified in 10% EDTA following Silva et al. (2011). Samples were then dehydrated through an ethanol series. We infiltrated each sample with the Electron Microscopy Science JB-4 embedding media protocol. Samples were sectioned at 3–4 µm using a glass knife. Sections were stained with Lee's Basic Fuchsin and Methylene Blue and imaged using an Olympus BX53 light microscope fitted with an Olympus DP80 camera (Olympus LS).

Results

Diet evolution

The ancestral state reconstruction of a diet indicated that the ancestor of *C. globiceps* and *C. recalvus* was most likely an invertivore (55%) but could have been an algivore (23%) or an anemone-feeder (22%) (Fig. 1). An alternative reconstruction indicated that the ancestor of the three *Clinocottus* species likely (94%) fed on "tentacles and appendages," which could have included barnacle cirri or anemone tentacles (Fig. S1). This scenario suggests that algivory is a more derived state in *C. globiceps* and *C. recalvus*, and may have evolved from an anemone-feeding ancestor.

Anemone-feeding behavior

We recorded 51 instances of *C. globiceps* attacking anemones. They struck the tentacles 40 times, the body column nine times, and the oral disc twice. Most strikes (98%), performed by all individuals of *C. globiceps*, were characterized by a consistent feeding behavior (Fig. 3). Specifically, *C. globiceps* approached the anemone, perched on its pelvic fins, and tilted laterally, constituting a preparatory phase. In a third of the preparatory phases, the fish hopped around the anemone, as if prospecting where to strike. In either case, *C. globiceps* then launched itself at the anemone while rolling up to 90 degrees about the long axis of its body. *Clinocottus globiceps* used suction to pull parts of the anemone into its mouth; then immediately rolled in the opposite direction while simultaneously pulling laterally and bending its body into a "C" shape (Fig. 3). Then the fish either pulled away from the anemone or performed additional rolling and bending motions, but in the opposite direction of the previous pull. *Clinocottus globiceps* commonly performed one (60%) or two sequential pulls (22%) and between three and 11 pulls in the remaining trials. In one outlier trial, *C. globiceps* performed 13 consecutive pulls, then transitioned to rotational feeding around the long axis of its body for 14 rotations before successfully tearing the anemone. Feeding events lasted between 0.11 and 1.5 s (mean ± SE: 0.29 s ± 0.04) from the start of the launch to when the fish withdrew.

We confirmed that *C. globiceps* was successful at removing pieces of the anemone in 23 trials (45%) based on visible tentacle or body damage. In 16 trials (31%), it was unlikely that *C. globiceps* was successful based on the lack of notable damage and the observation that the fish withdrew from the anemone with its mouth wide open. In contrast, the fish pulled away with their mouth closed during successful trials. In the remaining trials (23%), our view was obstructed, preventing reliable assessments. There appeared to be no correlation between successful feeding strikes and the number of pulls the fish performed.

We also recorded 40 strikes from three sculpin species feeding on fixed shrimp prey: seven by *C. globiceps*, 14 by *C. embryum*, and 19 by *O. maculosus*. The most observed behavior (47.5% of trials) from all species was a single lateral c-shaped pull that lacked the rolling motions of anemone feeding. In 25% of trials, the fish pulled two to three times with a pause between pulls. All three species also commonly used rotational feeding without a lateral pull to remove pieces of shrimp (27.5% of trials). Each species was observed performing each behavior at least once.

Feeding mechanics and morphology

Clinocottus globiceps and *C. recalvus* had feeding morphologies capable of producing a stronger bite than the other examined species (Fig. 4). The first principal component (PC 1, 52.8% of the variation) described variation in mechanical advantage, lower jaw dimensions, jaw occlusion, and tooth aspect ratio (Table S2). PC 2 (18.5% of the variation) described variation in quadrate offset, lower jaw dimensions, and premaxilla dimensions (Table S2). *Clinocottus globiceps* and *C. recalvus* occupied a region of the morphospace associated with shorter and wider lower jaws, higher mechanical

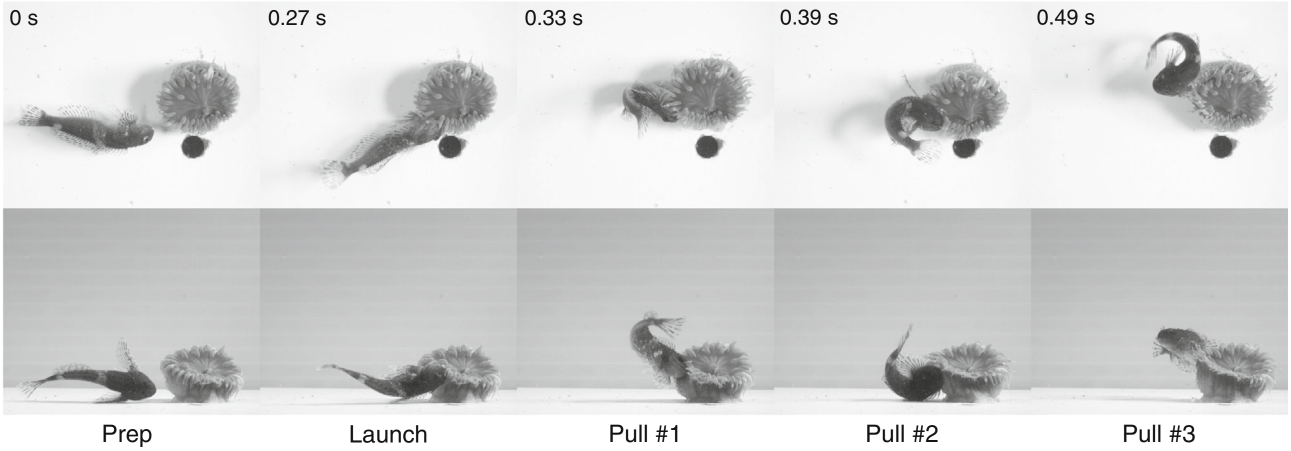

Figure 3 A representative video of *Clinocottus globiceps* feeding on an anemone from the dorsal (top) and lateral view (bottom). The animal starts in a titled preparatory phase then launches itself toward the anemone. In this trial, *C. globiceps* performs three consecutive pulls that involve rapid bending and rolling of the body. Full videos are available on FigShare, (Huie et al., 2025, https://figshare.com/s/b9200c27a9e715d31ade).

advantage, more crushing-like jaw occlusion, and higher tooth aspect ratios (Fig. 4). They also had proportionally larger jaw-closing muscle than all other species, but *C. globiceps* had slightly larger muscles than its sister species (Fig. 5). The other sculpins occupied regions associated with longer and narrower jaws, a shorter symphysis, and shorter premaxilla (Fig. 4). Separation along PC 2 indicated that *O. maculosus* had a longer and wider jaw and more slicing-like jaw occlusion than *C. embryum* and *O. triacis*.

Clinocottus globiceps and *C. recalvus* also shared a distinct dentition, including multiple rows of long teeth with flat, blade-like tips (Figs 4 and 6). In contrast, *C. embryum* and *O. maculosus* had primarily conical teeth. *Orthonopias triacis* also had predominantly conical teeth but possessed a row of blade-like teeth in the anterior portion of its jaw (Fig. 6e).

Histology

All species exhibited pliable lips with distinct structural features (Fig. 7). *Clinocottus globiceps* had thicker and more compact lip epithelium than all other species (Fig. 7e), except for *C. recalvus* (Fig. 7f). *Clinocottus globiceps* was the only species with ciliated epithelial cells covering its lips. Small goblet cells were sparsely distributed across the lip epidermis of all *Clinocottus* species (lowest in *C. globiceps*), whereas both small and enlarged goblet cells were confirmed in the lip epidermis of *O. maculosus* and *O. triacis*. In most species, the lip hypodermis was dominated by organized longitudinally aligned collagen fibers (Fig. 7e,g). However, the lips of *C. recalvus* were composed primarily of fatty, disorganized connective tissues with empty interstitial spaces (Fig. 7f). The dermis displayed a wavy, kinked pattern indicative of elastic tissue (Fig. 7f).

Inside the oral cavity, the epidermis covering the tooth-bearing regions of the jaws differed in topology and composition. In *C. embryum*, *O. maculosus*, and *O. triacis*, the epidermal layers formed numerous papillae that each contained a taste bud (Figs 6 and 7i). We observed only small goblet cells around the jaws, which were most abundant in *C. embryum*. Neither papillae, sensory cells, nor small goblet cells were observed in the jaw epithelium of *C. globiceps* or *C. recalvus*, which instead formed a thick shield over the jaws, perforated by the teeth (Figs 6 and 7h).

Clinocottus globiceps also lacked sensory and enlarged goblet cells in the epidermis on its face (Fig. 7a). All species had small goblet cells, but the other *Clinocottus* species had more than *C. globiceps* (Fig. 7b). Furthermore, the epidermis of *O. maculosus* and *O. triacis* were densely populated with enlarged goblet cells (Fig. 7c). Sensory cells were also observed in all species except *C. globiceps* and *C. recalvus* (Fig. 7b,c). The epidermis of the anterior region of the face was roughly the same thickness across species.

Discussion

We used a comparative framework to evaluate behavioral and morphological traits associated with anemone feeding in *Clinocottus globiceps*. Our results indicate that anemone feeding in *C. globiceps* involves a shift in feeding behavior and subtle changes to a suite of morphological traits. When compared to syntopic sculpin, *C. embryum* and *O. maculosus*, *C. globiceps* exhibits traits that could be adaptive for anemone-feeding, including a distinct combination of feeding behaviors defined by pulling, twisting, and bending as well as short, robust jaws for biting, and a comparatively thick lip to resist nematocyst stings. However, comparing *C. globiceps* to its sister species, *C. recalvus* (*sensu* Buser et al., 2017), anemone feeding does not appear to be associated with a unique feeding morphology. *Clinocottus recalvus* is primarily an algivore but largely shares the same suite of morphological traits as its anemone-feeding

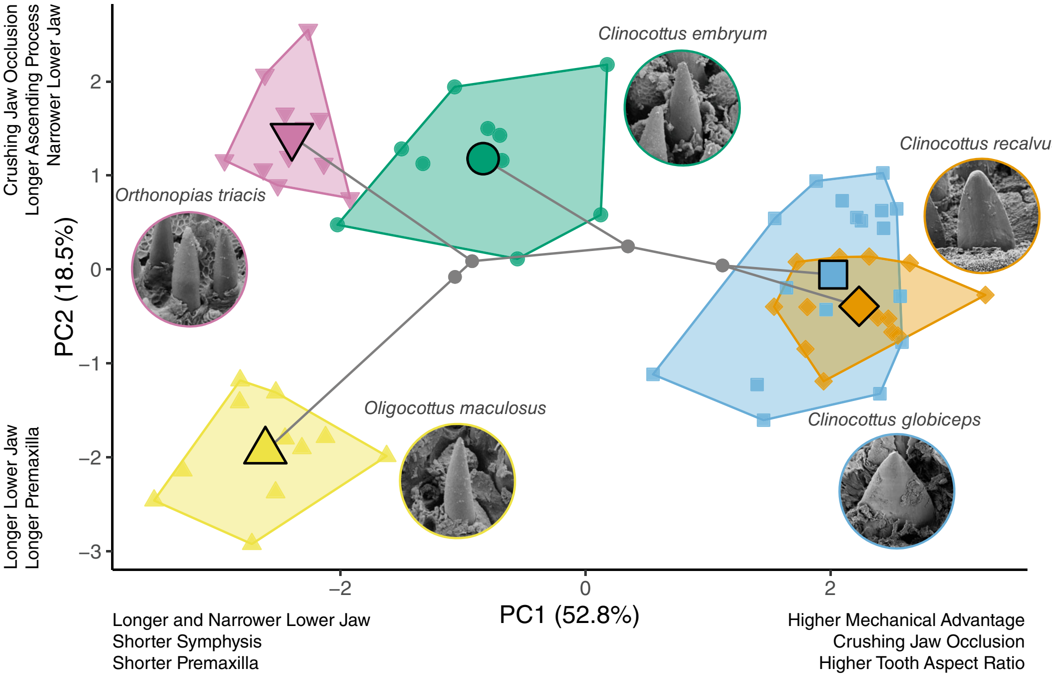

Figure 4 A phylomorphospace visualizing the variation in feeding mechanics and morphology of five sculpin species. Insets depict typical tooth shape for each species visualized with scanning electron microscopy. Large symbols depict the species means, while smaller symbols represent individual specimens (green square = *Clinocottus globiceps*, blue diamond = *C. recalvus*, orange circle = *C. embryum*, orange inverted triangle = *Orthonopias triacis*, orange triangle = *Oligocottus maculosus*).

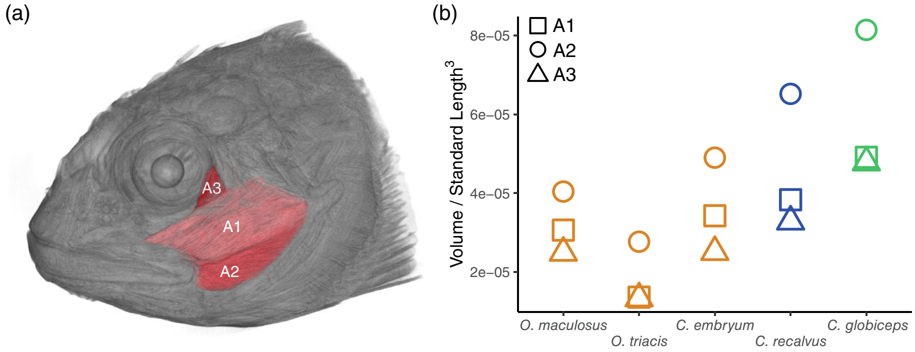

Figure 5 Variation in the volume of the jaw-closing muscles. (a) Reconstruction of the soft tissue anatomy of *Clinocottus globiceps* using diceCT. The subdivisions of the *adductor mandibulae* were segmented and measured for volume. (b) Dot plot depicting the variation in the relative volume of the individual subdivisions across species. Species colored by diet (green = anemone, blue = algae, orange = benthic arthropods).

sister. Only slight increases in the jaw-closing muscle and lip thickness were observed in *C. globiceps*, which may be artifacts of sample size rather than true differences. These findings suggest that the biting morphology of *C. globiceps* may have first evolved as an adaptation for scraping or tearing algae from rocks and was later co-opted for anemone feeding. That is further evidenced by the fact that *C. globiceps* also feeds substantially on algae (Grossman, 1986; Miller et al., 1980; Norton, 1995).

Prey acquisition is often attributed solely to actions carried out by the head, but postcranial regions also contribute significantly to successful feeding strikes (Camp et al., 2015; Camp & Brainerd, 2014; Kane & Higham, 2014, 2020; Perevolotsky et al., 2020). Changes in full body feeding behaviors may mitigate the need for specialized cranial kinematics (Kane, Cohen, et al., 2019; Kane, Roeder, et al., 2019). Thus, the unique combination of body and head movements employed by *C. globiceps* during anemone feeding might

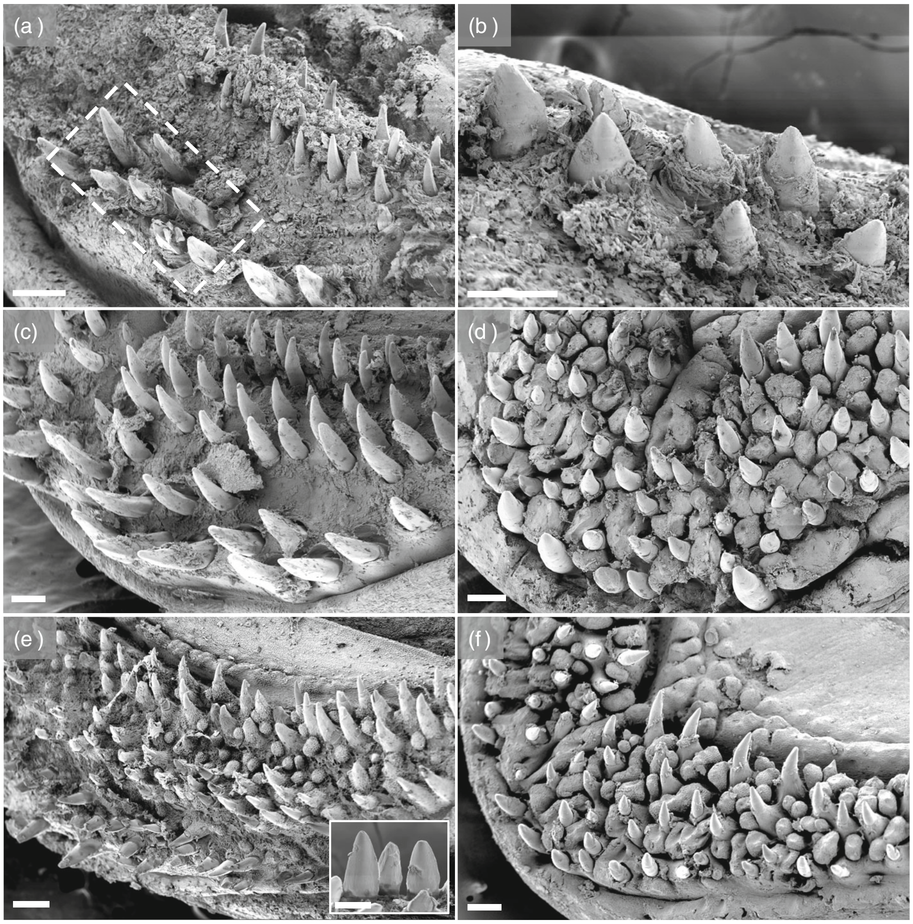

Figure 6 Dentition on the lower jaw of the five sculpin species. Dorsal view of (a) *Clinocottus globiceps*, (c) *C. recalvus*, (d) *C. embryum*, (e) *Orthonopias triacis*, and (f) *Oligocottus maculosus*. White box in (a) represents the region of the jaw shown in (b) from an oblique lingual view. The inset in (e) depicts a lingual view of the blade-like teeth at the anterior region of the jaw in *O. triacis* (scale bar = 50 μm). Scale bars (a–f) = 100 μm.

play a primary role in facilitating access to this resource. When presented with shrimp, the three syntopic sculpins employed a wide range of behaviors including rolling or pulling individually, but not all at once. Rolling about the long axis of the body is phylogenetically widespread for removing consumable pieces of food from larger chunks (Crawford et al., 2025; Helfman, 1990; Helfman & Clark, 1986). Because *C. globiceps* used the seemingly more complex rolling and pulling behavior to feed on anemone, there may be unique physical challenges associated with anemone feeding. For instance, the shrimp pieces were more friable and pulled apart easily, whereas anemone mesoglea is highly elastic. As a result, rolling (inflicting torsional stress) or pulling (inflicting tensile and shear stress) by themselves may be insufficient for tearing anemones. Stretching and twisting simultaneously probably improve the likelihood of success by weakening the tentacles' connection with the rest of the body.

Future endeavors should investigate the effects of fish size on anemone-feeding behaviors. Given that *C. globiceps* can grow to be 4× larger than the largest individual studied herein, larger individuals may not need to use the same feeding behaviors observed here. At larger sizes, the fish feed on small *Epiactis* anemones by removing them from the substrate entirely but appear to only graze on larger *A. elegantissima* (Yoshiyama, Wallace, et al., 1996). Thus, the anemone-feeding behavior and performance of *C. globiceps* may be dependent on predator size and prey traits.

Further investigations on algivory in *C. globiceps* and *C. recalvus* could help assess the novelty of the anemone-feeding behaviors. Other small to medium-sized fishes are capable of feeding on algae without using acrobatic behaviors (Cullen et al., 2013; Martinez et al., 2022; Rupp & Hulsey, 2014). These include algae-scraping blennies that bear a strong resemblance to *C. globiceps* and *C. recalvus* with their rounded face, high aspect ratio teeth, stout jaws, and thick lips (Egan et al., 2021; Hundt & Simons, 2018; Williams et al., 2022). The lip of *C. recalvus* is notably kinked, indicating that it is compliant and could aid in scraping by forming a better seal on irregular substrates (Evans et al., 2024).

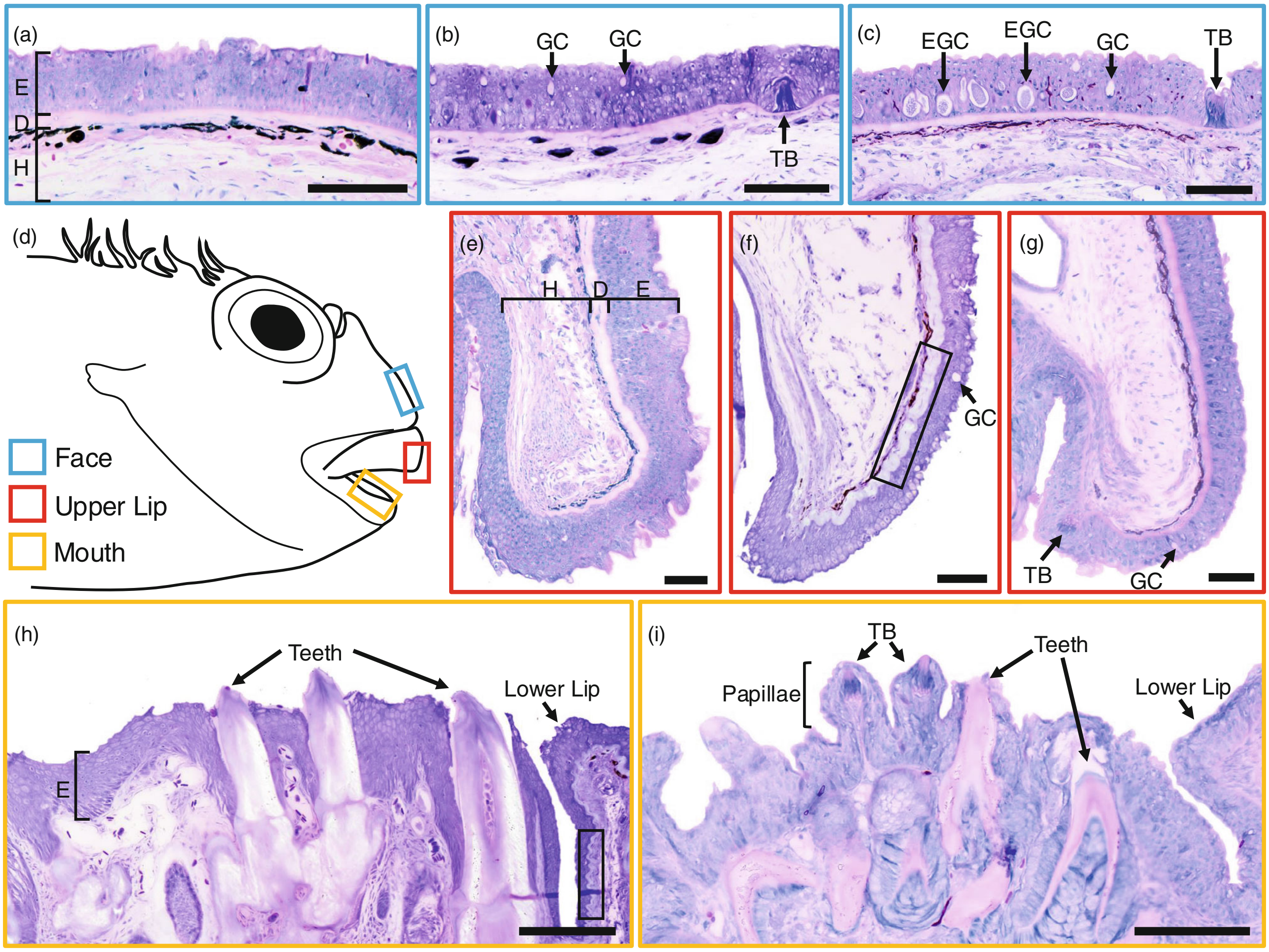

Figure 7 Representative histological variation in the face, lip, and mouth. Epidermis on the face of (a) *Clinocottus globiceps*, (b) *C. embryum*, and (c) *Oligocottus maculosus*. (d) A diagram depicting regions of the head that were sampled parasagittally. The upper lip of (e) *C. globiceps*, (f) *C. recalvus*, and (g) *O. maculosus*. Epidermis of the lower oral jaw in (h) *C. recalvus* (which is also representative of *C. globiceps*) and (i) *O. maculosus*. Abbreviations: D, dermis; E, epidermis; EGC, enlarged goblet cell; GC, goblet cell; H, hypodermis; TB, taste bud. Black boxes on F and H highlight sections of the wavy collagen in the dermis. Scale bars = 50 μm (a–c; e–g); 100 μm (h, i).

Together, the morphological similarities between algivorous blennies and sculpins provide indirect evidence that the synchronous twisting and pulling of *C. globiceps* is specific to feeding on anemones. Therefore, we propose that behavioral plasticity is important for transitions toward novel trophic niches like anemone-feeding. We also ask whether *C. recalvus* can exploit anemones using similar behaviors as *C. globiceps*. Investigations into the natural history of *C. recalvus* are needed to affirm it is strictly algivorous, which is currently informed by sparse diet data. If *C. recalvus* is indeed an anemone-feeder, then a reevaluation of the evolution of anemone-feeding in this clade is needed.

Anemone predators have developed structural and chemical adaptations to resist the effects of cnidarian nematocysts. Nudibranchs rely on mucus secretion to prevent nematocysts from discharging and epidermal spindle cells that provide structural defense (Greenwood et al., 2004; Martin et al., 2007). Similarly, corallivorous wrasses have folds on the outer surface of their thick lips that maximize mucosal secretion (Huertas & Bellwood, 2017, 2018). We observed a striking absence of goblet cells in and around the oral cavity, but we did find a relatively thick epithelium and fewer taste buds in *C. globiceps*. This morphology may physically shield sensitive tissues from nematocysts. However, *C. globiceps* will sometimes fail to remove pieces of anemone and withdraw with its mouth wide open (this study) or spit out pieces of *A. elegantissima* (Yoshiyama, Wallace, et al., 1996), indicating a potential negative reaction to nematocysts. Alternatively, failure may be elicited by an insecure grip on the anemone. In lab settings, smaller *C. globiceps* strike *Epiactis prolifera* more frequently than *A. elegantissima*, possibly because the former has a lower stinging potential (Yoshiyama, Wallace, et al., 1996). However, larger *C. globiceps* do not show preferences, emphasizing that fish size may affect sensitivity to nematocysts and, thus, feeding behaviors.

Substantial diversity exists among anemone-feeding fishes and medusivores more broadly (Ates, 1988, 1989). Butterflyfishes (Chaetodontidae) are the largest radiation of corallivorous and anemone-feeding fishes; however, cnidarian-feeding butterflyfishes share little in common with *C. globiceps*. The bluntface of *C. globiceps* is a stark contrast to the elongate snout of butterflyfishes (Konow et al., 2017; Motta, 1988). Additionally, *C. globiceps* has formidable blade-like teeth, while many chaetodontids have long, flexible, bristle-like teeth (Motta, 1988). Observations of butterflyfishes feeding on coral indicate the use of their forceps-like jaws to remove small polyps and scrape mucus (Motta, 1988). Anemone-feeding behaviors of butterflyfishes have not been described in detail, but some appear to tear pieces from anemones (Motta, 1988). In one instance, *Chaetodon auriga* was observed tearing a relatively small anemone entirely off the substrate using a head-flicking motion distinct from the feeding behavior of *C. globiceps* (pers. comm. Tal Perevolotsky). Lastly, we do not know how butterflyfishes resist cnidarian nematocysts, but their tolerance warrants further investigation (Wylie & Paul, 1989). Because traits related to prey acquisition in anemone-feeding fish appear diverse, we assert that multiple solutions can support this trophic niche.

So why is feeding on anemones uncommon as a trophic strategy? Anemone feeding may require adaptive changes to defense mechanisms in the throat and gut or specialized digestive physiology. Corallivorous butterflyfishes have longer guts than non-corallivores, likely reflecting adaptations for nutrient uptake (Berumen et al., 2011; Konow et al., 2017), since cnidarians are presumably nutrient poor (Berumen et al., 2011). We propose that longer guts could be a shared trait across anemone-feeding fishes and should be investigated in *C. globiceps*. Additionally, the propensity to evolve anemone-feeding behaviors may be restricted to specific evolutionary pathways. For example, when *C. globiceps* feeds on anemones, it preferentially targets individuals with endosymbiotic algae compared to those without (Augustine & Muller-Parker, 1998), suggesting an association with algivory could have played an important role in the transition toward anemone-feeding. This supports the hypothesis that *C. globiceps* was preadapted for anemone feeding since many herbivores also have longer digestive tracts (Arnette et al., 2024; German & Horn, 2006; Horn, 1989). In conclusion, reconstructing trophic evolution and comparing phenotypes across the diverse lineages of anemone-feeding fishes will help identify underlying causes and mechanisms that lead to this trophic novelty.

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Author contributions

JMH, TJB, and MAK conceived the ideas and designed methodology; JMH, SDA, KEC, and CHC collected the data; JMH, AJE, and KEC analyzed the data; EAK provided resources; JMH and SDA led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data availability statement

The datasets and R scripts supporting this article have been uploaded as part of the supporting information. Supporting videos were uploaded to FigShare (Huie et al., 2025, 10.6084/m9.figshare.28091066). All CT scans were uploaded to MorphoSource (see Table S1).

References

Arnette, S. D., Simonitis, L. E., Egan, J. P., Cohen, K. E., & Kolmann, M. A. (2024). True grit? Comparative anatomy and evolution of gizzards in fishes. *Journal of Anatomy*, **244**, 260–273.

Ates, R. M. L. (1988). Medusivorous fishes, a review. *Zoologische Mededelingen*, **62**(3), 29–42.

Ates, R. M. L. (1989). Fishes that eat sea anemones, a review. *Journal of Natural History*, **23**, 71–79.

Augustine, L., & Muller-Parker, G. (1998). Selective predation by the mosshead sculpin *Clinocottus globiceps* on the sea anemone *Anthopleura elegantissima* and its two algal symbionts. *Limnology and Oceanography*, **43**, 711–715.

Baliga, V. B., & Mehta, R. S. (2018). Phylo-allometric analyses showcase the interplay between life-history patterns and phenotypic convergence in cleaner wrasses. *The American Naturalist*, **191**, E129–E143.

Berumen, M. L., Pratchett, M. S., & Goodman, B. A. (2011). Relative gut lengths of coral reef butterflyfishes (Pisces: Chaetodontidae). *Coral Reefs*, **30**, 1005–1010.

Blackburn, D. C., Boyer, D. M., Gray, J. A., Winchester, J., Bates, J. M., Baumgart, S. L., Braker, E., Coldren, D., Conway, K. W., Rabosky, A. D., de la Sancha, N., Dillman, C. B., Dunnum, J. L., Early, C. M., Frable, B. W., Gage, M.

W., Hanken, J., Maisano, J. A., Marks, B. D., . . . Stanley, E. L. (2024). Increasing the impact of vertebrate scientific collections through 3D imaging: The openVertebrate (oVert) thematic collections network. *Bioscience*, **74**, 169–186.

Bollback, J. P. (2006). SIMMAP: Stochastic character mapping of discrete traits on phylogenies. *BMC Bioinformatics*, **7**, 88.

Boyer, D. M., Gunnell, G. F., Kaufman, S., & McGeary, T. M. (2016). Morphosource: Archiving and sharing 3-D digital specimen data. *Paleontological Society Papers*, **22**, 157–181.

Brezina, J. (1979). *Feeding studies on three species of fish from Tomales Bay, California*. University of the Pacific, Thesis. https://scholarlycommons.pacific.edu/uop_etds/2020

Bruhn, T., Schaller, C., Schulze, C., Sanchez-Rodriguez, J., Dannmeier, C., Ravens, U., Heubach, J. F., Eckhardt, K., Schmidtmayer, J., Schmidt, H., Aneiros, A., Wachter, E., & Béress, L. (2001). Isolation and characterisation of five neurotoxic and cardiotoxic polypeptides from the sea anemone *Anthopleura elegantissima*. *Toxicon*, **39**, 693–702.

Burge, R. T., & Schultz, S. A. (1973). *The marine environment in the vicinity of diablo cove with special reference to abalones and bony fishes*. California Department of Fish and Game.

Buser, T. J., Boyd, O. F., Cortés, Á., Donatelli, C. M., Kolmann, M. A., Luparell, J. L., Pfeiffenberger, J. A., Sidlauskas, B. L., & Summers, A. P. (2020). The natural Historian's guide to the CT galaxy: Step-by-step instructions for preparing and analyzing computed tomographic (CT) data using Cross-platform, open access software. *Integrative Organismal Biology*, **2**, obaa009.

Buser, T. J., Burns, M. D., & López, J. A. (2017). Littorally adaptive? Testing the link between habitat, morphology, and reproduction in the intertidal sculpin subfamily Oligocottinae (Pisces: Cottoidea). *PeerJ*, **5**, e3634.

Buser, T. J., Finnegan, D. L., Summers, A. P., & Kolmann, M. A. (2019). Have niche, will travel. New means of linking diet and Ecomorphology reveals niche conservatism in freshwater Cottoid fishes. *Integrative Organismal Biology*, **1**, obz023.

Buser, T. J., Kee, V. E., Terry, R. C., Summers, A. P., & Sidlauskas, B. L. (2023). Taurus of the tidepool? Inferring the function of cranial weapons in intertidal sculpins (Pisces: Cottoidea: Oligocottinae). *Ichthyology & Herpetology*, **111**, 98–108.

Camp, A. L., & Brainerd, E. L. (2014). Role of axial muscles in powering mouth expansion during suction feeding in largemouth bass (*Micropterus salmoides*). *The Journal of Experimental Biology*, **217**, 1333–1345.

Camp, A. L., Roberts, T. J., & Brainerd, E. L. (2015). Swimming muscles power suction feeding in largemouth bass. *Proceedings of the National Academy of Sciences of the United States of America*, **112**, 8690–8695.

Carrete Vega, G., & Wiens, J. J. (2012). Why are there so few fish in the sea? *Proceedings of the Royal Society B: Biological Sciences*, **279**, 2323–2329.

Cohen, K. E., Weller, H. I., & Summers, A. P. (2020). Not your father's homodonty—Stress, tooth shape, and the functional homodont. *Journal of Anatomy*, **237**, 837–848.

Collar, D. C., O'Meara, B. C., Wainwright, P. C., & Near, T. J. (2009). Piscivory limits diversification of feeding morphology in centrarchid fishes. *Evolution*, **63**, 1557–1573.

Crawford, C. H., Yadav, S., Huie, J. M., & Kane, E. A. (2025). Stop, chomp, and roll: Rotational feeding behavior in marine sculpins. *Northwestern Naturalist*, **105**(1), 54–58.

Cullen, J. A., Maie, T., Schoenfuss, H. L., & Blob, R. W. (2013). Evolutionary novelty versus exaptation: Oral kinematics in feeding versus climbing in the waterfall-climbing Hawaiian goby *Sicyopterus stimpsoni*. *PLoS One*, **8**, e53274.

Davies, K. T. J., Yohe, L. R., Almonte, J., Sánchez, M. K. R., Rengifo, E. M., Dumont, E. R., Sears, K. E., Dávalos, L. M., & Rossiter, S. J. (2020). Foraging shifts and visual preadaptation in ecologically diverse bats. *Molecular Ecology*, **29**, 1839–1859.

Egan, J. P., Buser, T. J., Burns, M. D., Simons, A. M., & Hundt, P. J. (2021). Patterns of body shape diversity and evolution in intertidal and subtidal lineages of Combtooth blennies (Blenniidae). *Integrative Organismal Biology*, **3**, obab004.

Evans, A. J., Naylor, E. R., Lujan, N. K., Kawano, S. M., & Hernandez, L. P. (2024). Deploy the proboscis! Functional morphology and kinematics of a novel form of extreme jaw protrusion in the hingemouth, *Phractolaemus ansorgii* (Gonorynchiformes). *Journal of Anatomy*, **244**, 929–942.

Fautin, D. G., Malarky, L., & Soberón, J. (2013). Latitudinal diversity of sea anemones (Cnidaria: Actiniaria). *The Biological Bulletin*, **224**, 89–98.

Ferry-Graham, L. A., Bolnick, D. I., & Wainwright, P. C. (2002). Using functional morphology to examine the ecology and evolution of Specialization1. *Integrative and Comparative Biology*, **42**, 265–277.

Ferry-Graham, L. A., Wainwright, P. C., Westneat, M. W., & Bellwood, D. R. (2001). Modulation of prey capture kinematics in the cheeklined wrasse *Oxycheilinus digrammus* (Teleostei: Labridae). *The Journal of Experimental Zoology*, **290**, 88–100.

Freeman, P. W. (1979). Specialized Insectivory: Beetle-eating and moth-eating Molossid bats. *Journal of Mammalogy*, **60**, 467–479.

German, D. P., & Horn, M. H. (2006). Gut length and mass in herbivorous and carnivorous prickleback fishes (Teleostei: Stichaeidae): Ontogenetic, dietary, and phylogenetic effects. *Marine Biology*, **148**, 1123–1134.

Grant, P. R., & Grant, B. R. (2002). Adaptive radiation of Darwin's finches: Recent data help explain how this famous group of Galápagos birds evolved, although gaps in our understanding remain. *American Scientist*, **90**, 130–139.

Greenwood, P. G., Garry, K., Hunter, A., & Jennings, M. (2004). Adaptable defense: A nudibranch mucus inhibits nematocyst discharge and changes with prey type. *The Biological Bulletin*, **206**, 113–120.

Grossman, G. D. (1986). Food resource partitioning in a rocky intertidal fish assemblage. *Journal of Zoology*, **1**, 317–355.

Helfman, G. S. (1990). Mode selection and mode switching in foraging animals. In P. Slater, J. S. Rosenblatt, & C. Beer (Eds.), *Advances in the Study of Behavior* (pp. 249–298). Academic Press.

Helfman, G. S., & Clark, J. B. (1986). Rotational feeding: Overcoming gape-limited foraging in anguillid eels. *Copeia*, **1986**, 679–685.

Higham, T. E., Ferry, L. A., Schmitz, L., Irschick, D. J., Starko, S., Anderson, P. S. L., Bergmann, P. J., Jamniczky, H. A., Monteiro, L. R., Navon, D., Messier, J., Carrington, E., Farina, S. C., Feilich, K. L., Hernandez, L. P., Johnson, M. A., Kawano, S. M., Law, C. J., Longo, S. J., … Niklas, K. J. (2021). Linking ecomechanical models and functional traits to understand phenotypic diversity. *Trends in Ecology & Evolution*, **36**, 860–873.

Horn, M. H. (1989). Biology of marine herbivorous fishes. *Oceanography and Marine Biology*, **27**, 167–272.

Huber, D. R., Dean, M. N., & Summers, A. P. (2008). Hard prey, soft jaws and the ontogeny of feeding mechanics in the spotted ratfish *Hydrolagus colliei*. *Journal of the Royal Society Interface*, **5**, 941–953.

Huertas, V., & Bellwood, D. R. (2017). Mucus-secreting lips offer protection to suction-feeding corallivorous fishes. *Current Biology*, **27**, R406–R407.

Huertas, V., & Bellwood, D. R. (2018). Feeding innovations and the first coral-feeding fishes. *Coral Reefs*, **37**, 649–658.

Huertas, V., & Bellwood, D. R. (2020). Trophic separation in planktivorous reef fishes: A new role for mucus? *Oecologia*, **192**, 813–822.

Huie, J. M., Arnette, S. D., Evans, A. J., Cohen, K. E., Buser, T. J., Crawford, C. H., Kane, E. A., & Kolmann, M. A. (2025). *Sculpin feeding videos*. Figshare. https://figshare.com/s/b9200c27a9e715d31ade

Huie, J. M., Thacker, C. E., & Tornabene, L. (2020). Co-evolution of cleaning and feeding morphology in western Atlantic and eastern Pacific gobies. *Evolution*, **74**, 419–433.

Hulsey, C. D. (2005). Function of a key morphological innovation: Fusion of the cichlid pharyngeal jaw. *Proceedings of the Royal Society B: Biological Sciences*, **273**, 669–675.

Hulsey, C. D., & León, F. J. G. D. (2005). Cichlid jaw mechanics: Linking morphology to feeding specialization. *Functional Ecology*, **19**, 487–494.

Hundt, P. J., & Simons, A. M. (2018). Extreme dentition does not prevent diet and tooth diversification within combtooth blennies (Ovalentaria: Blenniidae). *Evolution*, **72**, 930–943.

Johnston, R. F. (1954). The summer food of some intertidal fishes of Monterey County, California. *California Fish & Game*, **40**, 65–68.

Kane, E. A., Cohen, H. E., Hicks, W. R., Mahoney, E. R., & Marshall, C. D. (2019). Beyond suction-feeding fishes: Identifying new approaches to performance integration during prey capture in aquatic vertebrates. *Integrative and Comparative Biology*, **59**, 456–472.

Kane, E. A., & Higham, T. E. (2014). Modelled three-dimensional suction accuracy predicts prey capture success in three species of centrarchid fishes. *Journal of the Royal Society Interface*, **11**, 20140223.

Kane, E. A., & Higham, T. E. (2020). Kinematic integration during prey capture varies among individuals but not ecological contexts in bluegill sunfish, *Lepomis macrochirus* (Perciformes: Centrarchidae). *Biological Journal of the Linnean Society*, **130**, 205–224.

Kane, E. A., Roeder, M. M., DeRue, M. L., & Ghalambor, C. K. (2019). Integration between swim speed and mouth size evolves repeatedly in Trinidadian guppies and aligns with suction-feeding fishes. *Journal of Experimental Biology*, **222**, jeb190165.

Kass-Simon, G., & Scappaticci, A. A., Jr. (2002). The behavioral and developmental physiology of nematocysts. *Canadian Journal of Zoology*, **80**, 1772–1794.

Kikinis, R., Pieper, S. D., & Vosburgh, K. G. (2014). 3D slicer: A platform for subject-specific image analysis, visualization, and clinical support. In F. A. Jolesz (Ed.), *Intraoperative imaging and image-guided therapy* (pp. 277–289). Springer.

Koehl, M. A. R. (1977). Mechanical diversity of connective tissue of the Body Wall of sea anemones. *The Journal of Experimental Biology*, **69**, 107–125.

Kolmann, M. A., Huie, J. M., Evans, K., & Summers, A. P. (2018). Specialized specialists and the narrow niche fallacy: A tale of scale-feeding fishes. *Royal Society Open Science*, **5**, 171581.

Kolmann, M. A., Nagesan, R. S., Andrews, J. V., Borstein, S. R., Figueroa, R. T., Singer, R. A., Friedman, M., & López-Fernández, H. (2023). DiceCT for fishes: Recommendations for pairing iodine contrast agents with μCT to visualize soft tissues in fishes. *Journal of Fish Biology*, **102**, 893–903.

Konow, N., Price, S., Abom, R., Bellwood, D., & Wainwright, P. (2017). Decoupled diversification dynamics of feeding morphology following a major functional innovation in marine butterflyfishes. *Proceedings of the Royal Society B: Biological Sciences*, **284**, 20170906.

Martin, C. H., & Wainwright, P. C. (2011). Trophic novelty is linked to exceptional rates of morphological diversification in two adaptive radiations of Cyprinodon pupfish. *Evolution*, **65**, 2197–2212.

Martin, C. H., & Wainwright, P. C. (2013). Multiple fitness peaks on the adaptive landscape drive adaptive radiation in the wild. *Science*, **339**, 208–211.

Martin, R., Tomaschko, K.-H., & Walther, P. (2007). Protective skin structures in shell-less marine gastropods. *Marine Biology*, **150**, 807–817.

Martinez, C. M., Tovar, A. J., & Wainwright, P. C. (2022). A novel intramandibular joint facilitates feeding versatility in the sixbar distichodus. *Journal of Experimental Biology*, **225**, jeb243621.

Mihalitsis, M., & Bellwood, D. (2019). Functional implications of dentition-based morphotypes in piscivorous fishes. *Royal Society Open Science*, **6**, 190040.

Miller, B. S., Simenstad, C. A., Cross, J., Fresh, K., & Steinfort, S. N. (1980). *Nearshore fish and macroinvertebrate* *assemblages along the Strait of Juan de Fuca including food habits of the common nearshore fish*. Univ. Wash.

Motta, P. J. (1988). Functional morphology of the feeding apparatus of ten species of Pacific butterflyfishes (Perciformes, Chaetodontidae): An ecomorphological approach. *Environmental Biology of Fishes*, **22**, 39–67.

Nemeth, D. H. (1997). Modulation of attack behavior and its effect on feeding performance in a trophic generalist fish, *Hexagrammos decagrammus*. *The Journal of Experimental Biology*, **200**, 2155–2164.

Norton, S. F. (1995). A functional approach to ecomorphological patterns of feeding in cottid fishes. In J. J. Luczkovich, P. J. Motta, S. F. Norton, & K. F. Liem (Eds.), *Ecomorphology of Fishes* (pp. 61–78). Springer.

Perevolotsky, T., Martin, C. H., Rivlin, A., & Holzman, R. (2020). Work that body: Fin and body movements determine herbivore feeding performance within the natural reef environment. *Proceedings of the Royal Society B: Biological Sciences*, **287**, 20201903.

Porat, D., & Chadwick-Furman, N. E. (2004). Effects of anemonefish on giant sea anemones: Expansion behavior, growth, and survival. *Hydrobiologia*, **530**, 513–520.

Price, S. A., Wainwright, P. C., Bellwood, D. R., Kazancioglu, E., Collar, D. C., & Near, T. J. (2010). Functional innovations and morphological diversification in parrotfish. *Evolution*, **64**, 3057–3068.

R Core Team. (2023). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Revell, L. J. (2024). Phytools 2.0: An updated R ecosystem for phylogenetic comparative methods (and other things). *PeerJ*, **12**, e16505.

Rico-Guevara, A., Sustaita, D., Gussekloo, S., Olsen, A., Bright, J., Corbin, C., & Dudley, R. (2019). Feeding in birds: Thriving in terrestrial, aquatic, and aerial niches. In V. Bels & I. Q. Whishaw (Eds.), *Feeding in vertebrates: Evolution, morphology, behavior, biomechanics* (pp. 643–693). Springer International Publishing.

Rolfe, S., Pieper, S., Porto, A., Diamond, K., Winchester, J., Shan, S., Kirveslahti, H., Boyer, D., Summers, A., & Maga, A. M. (2021). SlicerMorph: An open and extensible platform to retrieve, visualize and analyse 3D morphology. *Methods in Ecology and Evolution*, **12**, 1816–1825.

Rupp, M. F., & Hulsey, C. D. (2014). Influence of substrate orientation on feeding kinematics and performance of algae grazing Lake Malawi cichlid fishes. *Journal of Experimental Biology*, **217**, jeb.105080.

Rutledge, K. M., Summers, A. P., & Kolmann, M. A. (2019). Killing them softly: Ontogeny of jaw mechanics and stiffness in mollusk-feeding freshwater stingrays. *Journal of Morphology*, **280**, 796–808.

Santana, S. E., & Cheung, E. (2016). Go big or go fish: Morphological specializations in carnivorous bats. *Proceedings of the Royal Society B: Biological Sciences*, **283**, 20160615.

Sazima, I. (1984). Scale-eating in characoids and other fishes. In T. M. Zaret (Ed.), *Evolutionary ecology of neotropical freshwater fishes: Proceedings of the 1st international symposium on systematics and evolutionary ecology of neotropical freshwater fishes, held at DeKalb, Illinois, U.S.A., June 14–18, 1982* (pp. 9–23). W. Junk Publishers.

Shick, J. M. (1991). *A functional biology of sea anemones*. Springer.

Silva, G., Moreira, A., & Alves, J. (2011). Histological processing of teeth and periodontal tissues for light microscopy analysis. *Methods in Molecular Biology*, **689**, 19–36.

Simenstad, C. A., & Nakatani, R. E. (1977). *Nearshore fish communities of Attu Island*. Alaska. https://digital.lib.washington.edu/researchworks/bitstream/handle/1773/3863/7714.pdf?sequence=1

Snook, L. B. (1997). *Aspects of the life history of Orthonopias tricis in Monterey Bay, California*. San Jose State University, San Jose, CA, USA.

Troyer, E. M., Evans, K. M., Goatley, C. H. R., Friedman, M., Carnevale, G., Nicholas, B., Kolmann, M., Bemis, K. E., & Arcila, D. (2024). Evolutionary innovation accelerates morphological diversification in pufferfishes and their relatives. *Evolution*, **78**(11), 1869–1882.

Turingan, R. G., & Wainwright, P. C. (1993). Morphological and functional bases of durophagy in the queen triggerfish, *Balistes vetula* (Pisces, tetraodontiformes). *Journal of Morphology*, **215**, 101–118.

Wainwright, P. C., & Richard, B. A. (1995). Predicting patterns of prey use from morphology of fishes. *Environmental Biology of Fishes*, **44**, 97–113.

Williams, K. L., Evans, K. M., & Simons, A. M. (2022). Tooth replacement and attachment morphology in the Pacific leaping blenny, *Alticus arnoldorum* (Blenniiformes: Blenniidae: Salariini) with a discussion on tooth function. *The Anatomical Record*, **305**, 1787–1803.

Wylie, C. R., & Paul, V. J. (1989). Chemical defenses in three species of *Sinularia* (Coelenterata, Alcyonacea): Effects against generalist predators and the butterflyfish *Chaetodon unimaculatus* Bloch. *Journal of Experimental Marine Biology and Ecology*, **129**, 141–160.

Yoshiyama, R. M., Knowlton, A. L., Welter, J. R., Comfort, S., Hopka, B. J., & Wallace, W. D. (1996). Laboratory behaviour of Mosshead sculpins *Clinocottus globiceps* toward their sea anemone prey. *Journal of the Marine Biological Association of the United Kingdom*, **76**, 793–809.

Yoshiyama, R. M., Wallace, W. D., Burns, J. L., Knowlton, A. L., & Welter, J. R. (1996). Laboratory food choice by the mosshead sculpin, *Clinocottus globiceps* (Girard) (Teleostei; Cottidae), a predator of sea anemones. *Journal of Experimental Marine Biology and Ecology*, **204**, 23–42.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1 List of specimens examined with μCT, their catalog numbers, MorphoSource links, and morphological measurements.

Table S2 Loadings from the principal component analysis.

Figure S1 Ancestral state reconstruction of diet using a modified version of the synthetic diet classifications from Buser et al. (2019).

Data S1 The R scripts and supporting files (.R file, .tree file, and Table S1.csv) needed to conduct and visualize the morphological analyses conducted in this study.