Behavioral drive and morphological amplification of an aggressive display

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The evolution of conspicuous morphology and related displays is often ascribed to their role in sexual selection. The context of displays together with the phylogenetic sequence of morphological and behavioral innovations provides insight into their evolution. Do conspicuous features function in mate attraction and/or aggression and does a behavioral display evolve before or after the morphological feature most evident in the display? These questions were explored for a unique display and dorsal fin feature in a clade of blenniiform fishes for which both courtship and aggressive displays are known. The anterior dorsal-fin spines of the Spikefin Blenny, *Coralliozetus rosenblatti*, are elongate. It has a unique courtship display but the fin is held statically erect similar to congeners. This and other species of *Coralliozetus*, perform a unique aggressive display, the "fin flag", in which the anterior dorsal fin is waved laterally when encountering conspecifics. The spike-like dorsal fin of *C. rosenblatti* and its exaggerated lateral movements render this display especially conspicuous. In addition, it performs the fin flag more than twice as often as congeners. Thus, the dorsal fin of the Spikefin Blenny evolved to amplify an extant aggressive display consistent with the *behavioral drive* hypothesis that posits behavior leads to subsequent morphological evolution making displays more effective.

KEYWORDS

behavioral drive, displays, amplification, aggression, courtship, Chaenopsidae, Blenniiformes, Teleostei

Introduction

Conspicuous morphological features of animals and the behaviors displaying them are often attributed to their role in sexual selection, either for attracting mates, aggressive signaling in intraspecific interactions, or both (Andersson, 1994; Berglund et al., 1996; Laidre and Johnstone, 2013). Identifying which of these is the proper context of conspicuous displays can be inferred by observing the frequency of such displays during aggressive versus courtship interactions, but the origin of such displays and the morphology upon which they are based is more elusive. Comparison of morphology and behavior across species sharing a recent common ancestor (clades) is a valuable approach

to understanding the origin and modification of both morphology and associated behaviors displaying that morphology (McLennan et al., 1988; Wcislo, 1989; Prum, 1990; Martins, 1996; Ord and Martins, 2010; Johnson et al., 2019).

A phylogenetic approach also provides promise for understanding the coevolution of morphology and behavior. Do unique morphological features evolve before behaviors displaying the feature (morphological drive) or do behaviors evolve first followed by morphology featuring or amplifying those displays (behavioral drive; Bateson, 1988; Wcislo, 1989; Bateson, 2004; Duckworth, 2009; Wcislo, 2021)? These questions can be addressed for groups in which both morphology and behavioral displays are known, and whose species-level phylogeny has been hypothesized (Wcislo, 1989). Behavioral drive is supported when associated morphological features evolve after the origin of a particular behavior, i.e., when the behavior is present in ancestors that do not share the morphology. Morphological drive is supported if ancestors possess a morphological feature used in displays by descendant species. Evolution of both behavior and morphology at the same point on a phylogenetic hypothesis cannot discriminate between the two (Wcislo, 1989). This study addresses these questions in a small clade of blenniiform fishes for which a behavioral inventory of aggressive and courtship displays and a species-level phylogenetic hypothesis are available.

Tube blennies of the genus *Coralliozetus* (Teleostei, Blenniiformes, Chaenopsidae) are a morphologically and genetically distinctive lineage found on shallow reefs in the tropical eastern Pacific (six species) and Caribbean (one species; Hastings, 1997; Lin and Hastings, 2011; Hastings, 2021). Typical of tube blennies, the species of *Coralliozetus* occupy vacant tests of invertebrates that are essential for survival (Hastings and Galland, 2010) and are necessary resources for male reproductive success (Hastings, 1986; Hastings and Petersen, 2010). They have a polygynous mating system in which females deposit demersal eggs in the shelters of males and eggs are guarded by the resident male until hatching (Hastings, 1986; Hastings, 1988; Hastings and Petersen, 2010). Males must defend shelters from competing males and also attract females to their shelters for mating. Consequently, shelters are highly contested by males and a surprising variety of aggressive displays and conspicuous courtship displays characterize the group (Hastings, in prep.). As a consequence, these fishes provide a convenient group to study the co-evolution of morphology and display behavior.

One species, the so-called Spikefin Blenny (*Coralliozetus rosenblatti*), is endemic to the Gulf of California and possesses a unique (for the genus) dorsal fin in which the anterior three spines of males are prolonged (Figure 1), the longest being at least twice as long as more posterior spines (Stephens, 1963; Hastings, 2019). The anterior dorsal fin of males of most congeners is even in shape in that all spines are similar in length (in *C. angelicus*, *C. boehlkei*, *C. cardonae*, *C. springeri* and *C. clausus*), while the dorsal fin of *C. micropes* is sail-like with all spines prolonged (Figure 1). This study addresses two questions regarding the evolution of this autapomorphy in *C. rosenblatti*. First, what is the context of displays revealing the unique spike-like dorsal fin of *C. rosenblatti*? Is the dorsal fin presented in a unique or exaggerated way during courtship displays, aggressive displays or both? Second, did the evolution of the spike-like dorsal fin predate the evolution of any associated display, consistent with morphological drive, or did the behavior evolve before the morphology, consistent with the behavioral drive hypothesis? In order to address these questions both courtship and aggressive displays were recorded for the species of *Coralliozetus* and the outgroup species *Protemblemaria bicirris* and observed character states were mapped on a species-level phylogenetic hypothesis.

Methods

Behavioral recordings

A video inventory of displays by six species of *Coralliozetus* and the outgroup *Protemblemaria bicirris* was assembled from a larger survey of display behaviors in chaenopsids (Hastings, in prep.). This was accomplished during visits to field stations within the range of each species. This included ITESM - Guaymas, Sonora, Mexico for *C. angelicus*, *C. micropes*, *C. rosenblatti*, and *P. bicirris*, CIAD, Mazatlán, Mexico for *C. boehlkei*, and STRI - Naos, Panama for *C. springeri*, and Bocas del Toro, Panama for *C. cardonae* (specimens transported to and videos recorded at STRI - Naos). At each site, males and females were captured alive using plastic bags while snorkeling and returned to the lab were they were established in aquaria with substrates and shelters similar to those inhabited by the species in the wild. Shelters included barnacle tests for *C. angelicus*, *C. cardonae*, *C. springeri* and *P. bicirris*, and worm and vermetid gastropod tubes for *C. boehlkei*, *C. micropes* and *C. rosenblatti*. Study animals were fed live or frozen brine shrimp or flake food. After acclimation of several hours to a day individuals were video recorded for varying lengths of time. Solitary males were allowed to occupy vacant shelters and, in order to elicit aggressive displays, one or more additional males were added to aquaria, while courtship was elicited by adding a female. Video sequences of interactions were obtained using a Canon analog video system at 30 frames per second and later converted to digital format. Voucher specimens were deposited in the Marine Vertebrate Collection at Scripps Institution of Oceanography (SIO). Videos of a recently described species of *Coralliozetus* endemic to Isla del Coco, Costa Rica (Hastings, 2021) are unavailable.

Character scoring and mapping

The shape of the anterior dorsal fin, form of courtship displays, position of the dorsal fin during courtship displays, and all aggressive displays were described for the species of *Coralliozetus* and *P. bicirris*. The presence/absence of one notable aggressive display, the "fin flag", known only within the genus *Coralliozetus* and *P. bicirris*, was mapped on a phylogenetic hypothesis for the family Chaenopsidae (Hastings, 2019) using Mesquite (Maddison and Maddison, 2017). For *P. bicirris* and six species of *Coralliozetus*, the number of separate male/male interactions where one male
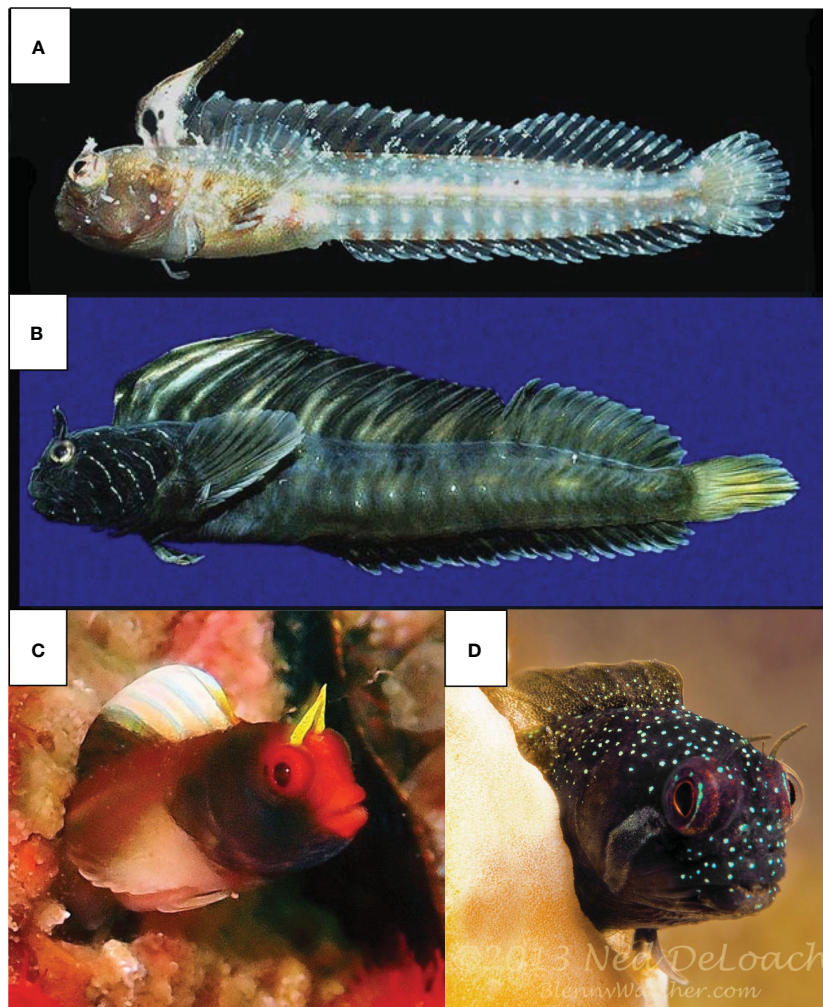
FIGURE 1
Dorsal fins of males of selected species of *Coralliozetus*. **(A)** *C. rosenblatti* with elongate anterior dorsal-fin spines; **(B)** *C. micropes* with sail-like dorsal fin; **(C)** *C. angelicus* and **(D)** *C. cardonae* with even dorsal fins. Photos reprinted with permission from **(A, B)** G. R. Allen (Source: D. R. Robertson and G. R. Allen. 2015. Shorefishes of the Tropical Eastern Pacific: online information system); **(C)** R. Woheau (Source: Mexican-fish.com); **(D)** N. DeLoach.

closely approached another and the number of these interactions that elicited a fin-flag display by either of the males were recorded.

Results

Dorsal-fin shape of male chaenopids

The shape of the dorsal fin of males of most species of chaenopsids is more-or-less even with all spines similar in length (Hastings, 2019). This includes *P. bicirris* and four species of *Coralliozetus* (Table 1; Figure 1). In *C. micropes* the dorsal fin of males is large and sail-like, similar to that in several members of *Emblemaria* and *Chaenopsis* (Hastings, 2019). In *C. rosenblatti* the dorsal fin of males is spike-like with the anterior three spines longer than more posterior spines (Figures 1, 2; Stephens, 1963). A somewhat similar dorsal fin with elongate anterior spines evolved independently in selected species of *Emblemariopsis* and one species of *Emblemaria* (Hastings, 2019).

Courtship displays

Male chaenopsids often court when they see a female near their shelter and when they see surrounding males courting (Hastings, 1988). Courtship displays typically involve a conspicuously colored resident lunging in and out of their shelter. The most common pattern in the family is the "jack-in-the-box" display in which males lunge directly outward and immediately withdraw backwards, directly into the shelter. Variation across species is seen in the speed of individual lunges and thus the duration of a single lunge, the frequency of lunges, the outward extent of each lunge, movement of the head during lunges, and movement and position of the dorsal and pelvic fins during lunges (Hastings, in prep.).

In three of the species of *Coralliozetus* the male lunges outward from the shelter approximately two thirds of his body length (i.e., the tail region remains in the shelter) and the anterior body drops downward before being withdrawn into the shelter, here termed "lunge-and-fall" (Table 1). *Coralliozetus angelicus* extends the

TABLE 1 Form of courtship displays and shape and position of the dorsal fin during courtship lunges in *Coralliozetus* species and *P. bicirris*.

Species	Courtship Display	Dorsal Fin Shape and Position During Courtship
Coralliozetus angelicus	Bob-and-weave	Even; Static erect
Coralliozetus boehlkei	Lunge-and-fall	Even; Static erect
Coralliozetus cardonae	Lunge with head snap	Even; Static erect
Coralliozetus micropes	Lunge-and-fall	Sail-like; Static erect
Coralliozetus rosenblatti	Hesitating lunge	Spike-like; Static erect
Coralliozetus springeri	Lunge-and-fall	Even; Static erect
Protemblemaria bicirris	Lateral head shake	Even; Inside shelter

amount of time outside of the shelter and with each lunge does a "bob-and-weave" movement in which the head and anterior body are moved side to side and up and down while the posterior body maintains contact with the shelter. Courtship in *C. cardonae* is unique in that males rapidly lunge partially outward from the shelter and snap the head to the side upon retreat ("lunge with head snap"). Courtship in *C. rosenblatti* is also unique in that the male lunges a half body length outward, pauses, and lunges further, pausing again before fully retracting into the shelter ('hesitating lunge"; Supplementary Video 1). Courtship in *P. bicirris* differs from all of these and involves a short outward lunge with only the head protruding from the shelter and a rapid side-to-side shaking of the head. In these six species of *Coralliozetus*, including *C. rosenblatti*, the dorsal fin is held statically erect during each lunge and folded downward when retracting into the shelter (Table 1).

Aggressive displays

As far as known, all chaenopsids perform two basic displays in intraspecific aggressive interactions. The first is "branchial flare" in which the branchial chamber is expanded ventrally and laterally by lowering the urohyal region and flaring the opercular series (Lindquist, 1971). The second is "dorsal-fin erection" in which the anterior dorsal fin is held fully and statically erect and presented toward an intruder. Variations of these ubiquitous displays account for a surprising array of aggressive displays in these fishes (Hastings, in prep.).

One of the variations of "dorsal-fin erection" is "fin flag" in which the anterior dorsal-fin spines are repeatedly moved laterally, both to the left and to the right, when encountering a conspecific (Figure 2; Supplementary Videos 2–4). This display is performed by non-resident (those outside of a shelter) and resident males (inside a shelter) when closely approached by a conspecific. Among the 25 chaenopsid species surveyed (Hastings, in prep.), this fin-flag

display was observed only in *P. bicirris* and five of the species of *Coralliozetus* (Table 2). This display was not observed in *C. angelicus* creating uncertainty of the precise evolutionary history of this display although evidence indicates that the display was present in the ancestor of the four species clade that includes *C. rosenblatti* (Figure 3).

In the species with an even dorsal fin and in *C. micropes* with a sail-like fin (i.e., all except the Spikefin Blenny), lateral movements resemble a waving flag with movement greatest anteriorly and increasingly dampened more posteriorly through the first several spines (Supplementary Videos 3, 4). In the Spikefin Blenny the lateral movement is largely restricted to the elongate anterior spines. Also, the extent of lateral movement of the anterior spines is greatest in *C. rosenblatti* and may be as much as 180 degrees (Figure 2; Supplementary Video 2).

These species vary in the frequency of this display, performing it rarely, to in about one in four or five male-male encounters, to one in three in *P. bicirris* (Table 2). The greatest frequency of this display is seen in the Spike-fin Blenny that performs the fin-flag display in nearly two out of every three male-male encounters. Species that perform this display often have distinctive coloration on the anterior fin spines that are moved laterally (see Figure 1).

Discussion

The dorsal fin of the Spikefin Blenny appears to have evolved in the context of aggression rather than courtship. While this species performs a unique courtship display ("hesitating lunge"; Supplementary Video 1), during these lunges the dorsal fin is held rigidly erect as it is in all other species of *Coralliozetus* (Table 1). Although evident during courtship the elevated dorsal fin is not displayed in a unique way and does not involve a unique movement of the fin. While it may function in species recognition, it does not contribute to a unique form of courtship display.

Instead, the spike-like fin appears to have evolved in context of aggression. The fin of this species is especially evident in an aggressive display common to four other species of *Coralliozetus* and *P. bicirris*. The fin-flag display reaches its highest expression in terms of both frequency and extent of lateral fin movement in *C. rosenblatti*. This species' elongate anterior dorsal-fin spines make this display especially conspicuous and the extent of lateral movement of the dorsal fin is both unique and extraordinary. In addition, this display is performed in the majority of male-male encounters (Table 2). These observations are consistent with the hypothesis that the elongation of the anterior spines of this species evolved to amplify (*sensu* Hasson, 1990) the fin-flag display.

A few other species in other lineages of chaenopsids have independently evolved elongate anterior dorsal-fin spines (Hastings, 2019), but as far as known these species do not perform the aggressive fin-flag display. For example, *Emblemariopsis signifera* has elongate anterior dorsal-fin spines that appear to function in crypsis. This species moves the anterior dorsal fin side to side and in a circular motion after short swimming movements when outside of shelters (Hastings, in prep.). These movements of the fin resemble the motion of algae and other

FIGURE 2
Frame grabs from an approximate three-second interval of a fin-flag display in *Coralliozetus rosenblatti* (see Supplementary Video 2 for source of these images). Time proceeds down the left column, then down the right column of images. The last two elements of the time code represent seconds and frames (30 frames per second). The focal male is facing the camera and displaying to an intruder in the upper left of each image. Note left and right lateral (transverse) movements of the anterior dorsal fin are nearly 180 degrees.

TABLE 2 Proportion of male-male encounters that involved an aggressive fin-flag display by one of the participants.

Species (number of males observed)	N	Number with fin-flag display	Percent with fin-flag display
Coralliozetus angelicus (15)	26	0	0%
Coralliozetus boehlkei (31)	64	13	20%
Coralliozetus cardonae (11)	15	1	7%
Coralliozetus micropes (10)	21	5	24%
Coralliozetus rosenblatti (14)	26	16	62%
Coralliozetus springeri (9)	17	3	18%
Protemblemaria bicirris (4)	42	13	31%

Numbers in parentheses indicate the number of males observed; N, number of unique encounters observed.

filamentous items in the benthic reef environment and may function in crypsis.

Aggressive displays in fishes often involve static erection of the dorsal fin for example in poeciliids (Goldberg et al., 2019) or repeated flashing of the dorsal fin such as in the blenniid *Alticus* (Ord and Hsieh, 2011). However, the dorsal-fin spines of most acanthopterygian fishes have limited lateral movement and the extent of lateral movement seen in these tube blennies is extraordinary. This appears to be facilitated by the interlocking ring-like structures between the base of the dorsal-fin spines and each supporting pterygiophore in species of *Coralliozetus* (Hastings, 1997: see character 18, Figure 2E). This permits movement of the spines in both the medial and transverse planes.

The fin-flag was not observed in *C. angelicus*. While not observing a display behavior in a particular species is not strong evidence of its absence (Foster, 2013; Foster and Baker, 2019), the possible absence of this display may be related to this species'
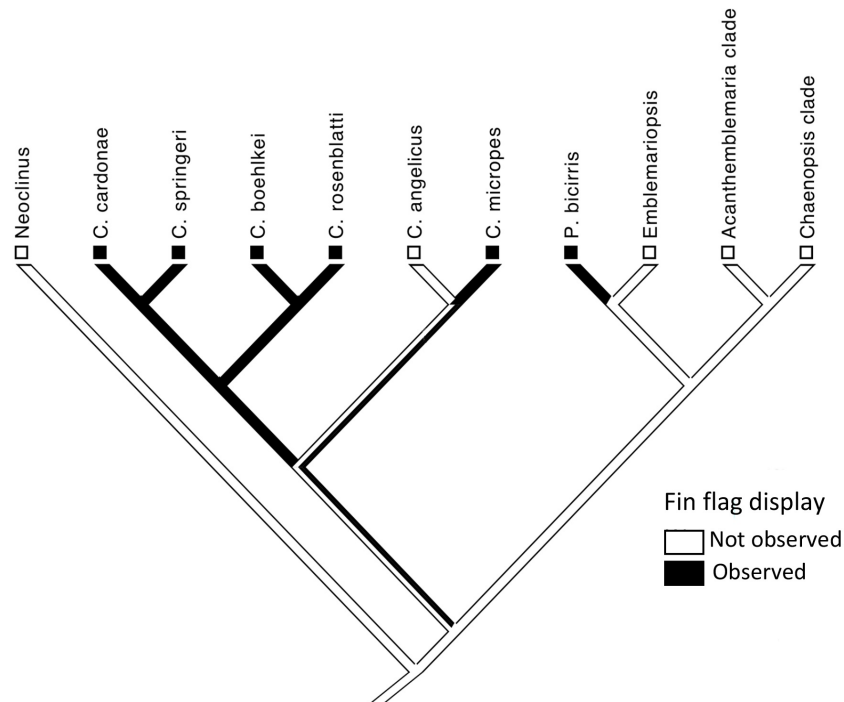
FIGURE 3
Character map for presence of the fin-flag display in chaenopsid blennies. Phylogeny is after Hastings (2019).

microhabitat. The Angel Blenny occupies vacant barnacle tests in high surge zones (Hastings, 1988) where intentional lateral movement of the fin may be constrained.

Consistent with the behavioral drive hypothesis, evolution of the spike-like dorsal fin in *C. rosenblatti* occurred after the origin of the fin-flag display. The unique shape of the fin together with its exaggerated lateral movements serve to amplify (*sensu* Hasson, 1990) this extant aggressive display.

Behavioral drive posits that individuals with phenotypic variation in a morphological feature that makes an extant behavior more effective or more efficient gain a selective advantage and over time the feature becomes fixed (Bateson, 1988; Bateson, 2004; Duckworth, 2009; Wcislo, 2021). While some behaviors may be a constraint (Huey et al., 2003), others are hypothesized to have led to subsequent morphological evolution (reviewed in Wcislo, 1989; Wcislo, 2021). Although relatively few studies have explicitly invoked behavioral drive as a mechanism of display evolution it is likely to have played a significant role in amplification of a variety sexually selected characters (Hasson, 1991). This includes amplifying or making more conspicuous the courtship plumage of male manakins (Prum, 1990) and increased nuptial coloration in male sticklebacks (McLennan, 1990). Behavioral drive may also account for the evolution of aggressive display features such as the increased head width in Hawaiian *Drosophila* species that first evolved a unique head-to-head fighting posture (Spieth, 1981). Similarly, the elongation and conspicuous coloration of the jaws in the Sarcastic Fringehead blenny (*Neoclinus blanchardi*) have been shown to amplify an extant aggressive gaping display (Hongjamrassilp et al., 2018). Additional phylogenetic studies on the evolutionary sequence of display behaviors and

their revealed structures are needed to more fully document the role of behavioral drive in display evolution.

Data availability statement

The datasets presented in this article are not readily available because all data are included in the article. Requests to access the datasets should be directed to phastings@ucsd.edu.

Ethics statement

The animal study was approved by UCSD Institutional Animal Care and Use Committee (IACUC). The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

PH: Writing – original draft, Writing – review & editing, Conceptualization, Investigation, Funding acquisition.

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Conflict of interest

The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fetho.2023.1325273/full#supplementary-material

SUPPLEMENTARY VIDEO 1
Courtship in *Coralliozetus rosenblatti*. The 'hesitating lunge' is unique to this species. As in other tube blennies, the dorsal fin is held erect during the courtship display but not moved in a unique way in this species. Recorded at ITESM of a specimen collected in the Guaymas, Sonora, Mexico region (voucher: SIO 04-172).

SUPPLEMENTARY VIDEO 2
Fin-flag display in *Coralliozetus rosenblatti*. Focal male is displaying to intruder in the upper left of images. Recorded at ITESM of specimens collected in the Guaymas, Sonora, Mexico region (vouchers: SIO 04-172 and SIO 04-173).

SUPPLEMENTARY VIDEO 3
Fin-flag display in *Coralliozetus boehlkei*. Focal male is displaying to male in shelter in lower right of images. Recorded at CIAD-Mazatlán of specimens collected in the Mazatlán, Sinaloa, Mexico region (vouchers: SIO 20-16).

SUPPLEMENTARY VIDEO 4
Fin-flag display in *Protemblemaria bicirris*. Focal male is displaying to a male in the barnacle in lower right of images. Recorded at ITESM of specimens collected in Guaymas, Sonora, Mexico region (vouchers: SIO 04-172 and SIO 04-173).

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