Johnson, G.D., Collins, R.A. & Brothers, E.B. (2025) Putative Batesian mimicry of gelatinous zooplankton by larvae of marine fishes: a closer look based on in-situ images by blackwater photographers. *Journal of the Ocean Science Foundation*, 42, 91–119.

doi: https://doi.org/10.5281/zenodo.14889573

Corrigendum

PAGE 93: Note that the caption for Figure 1 should be revised to:

Figure 1. Extensive head and fin-ray spination offers mechanical predator deterrence: (clockwise from bottom left) fixed specimens of *Ranzania, Gonioplectrus, Naso, Forcipiger, Masturus, Hoplolatilus, Holocentrus, Anoplogaster*, and *Chaetodon* (all DJ), plus *Epinephelus*, live (at center) (LI).

PAGE 114: The first photographer credit in Figure 32 is changed from DW to WS:

Figure 32. Putative mimicry by *Astronesthes* (upper left) (WS); its coiled gut shows a conspicuous similarity to the coiled tentacles of hydrozoans *Olindias tenuis* (top right) (RC), *Cirrhitiara superba* (lower right) (RC), and *Eutiara mayeri* (lower left) (LI).

Journal of the
Ocean Science Foundation

2025, Volume 42

Putative Batesian mimicry of gelatinous zooplankton by larvae of marine fishes: a closer look based on in-situ images by blackwater photographers

G. DAVID JOHNSON*
*(*deceased) Department of Vertebrate Zoology, National Museum of Natural History,*
Smithsonian Institution, Washington, DC 20560, USA
https://orcid.org/0000-0003-4339-6589

RICHARD A. COLLINS
Florida Museum of Natural History, University of Florida, Gainesville, FL 33004, USA
https://orcid.org/0000-0002-6225-444X   E-mail: richard.collins@floridamuseum.ufl.edu

EDWARD B. BROTHERS
EFS Consultants, Ithaca, NY, USA   E-mail: ghotti@gmail.com

Abstract

Examination of photographs and videos of living epipelagic oceanic larval fishes and invertebrates obtained during night dives provided heretofore unavailable information on the appearance and behavior of these organisms. The raw data were provided by numerous "blackwater" divers in oceans around the world. Extraordinary elaborations of fin rays, body form, and other morphological features of the fishes were observed to present similarities in appearance to common noxious, unpalatable, and low-energy content invertebrates in the same environment, especially cnidarians. Much has been written about the possible functions of these structures, with the recognition that they must come at a price in terms of active predator avoidance, i.e. they create varying levels of drag and thus inhibit rapid swimming and maneuvering. Among the most commonly suggested of these is Batesian mimicry of toxic or "nutritionally barren" gelatinous zooplankton such as jellyfish and siphonophores. These observations support the previously suggested hypothesis that many highly predation-vulnerable larval fishes are gaining protection by resembling unpalatable and dangerous invertebrates. This mechanism is one of several ways larval fishes may avoid predation. Evidence for Batesian mimicry is further supported by observations of direct associations between fishes (and some vulnerable invertebrates) and cnidarians. This phenomenon is designated as protective commensalism. Batesian mimicry by oceanic larval fishes appears to have evolved in at least 15 orders and dozens of families of fishes. Many examples of potential mimic and model pairs are illustrated here in photographs. The study concludes with some suggestions for future work on documenting and understanding the origin and nature of Batesian mimicry in the early life history of marine fishes.

Key words: jellyfish, ichthyology, commensalism, coral reef fishes, invertebrates, ctenophores, cnidarians

Citation: Johnson, G.D., Collins, R.A. & Brothers, E.B. (2025) Putative Batesian mimicry of gelatinous zooplankton by larvae of marine fishes: a closer look based on in-situ images by blackwater photographers. *Journal of the Ocean Science Foundation*, 42, 91–119.

doi: https://doi.org/10.5281/zenodo.14889573

Introduction

Compared to the underlying depths, the shallower epipelagic zone of the open ocean is a high-energy, nutrient-rich regime that supports a myriad of planktonic life forms and serves as a nursery ground for many. Among the latter are the early life stages of marine fishes that, as adults, occupy diverse habitats ranging from shallow inshore waters to the deep reaches of the abyss, encompassing all habitats in between. Most of these habitats are fundamentally different from the epipelagic zone, and this is reflected in the diverse morphologies of the adults. The larvae of most of these marine fishes differ strikingly from the adults, having evolved to be successful in the relatively uniform, ubiquitous planktonic arena. Despite this environmental uniformity, these larval forms exhibit a remarkable array of morphological diversity which has captured the fancy and moved the pen of ichthyologists and evolutionary biologists since their earliest descriptions.

In recent years, the development of blackwater diving has opened a new window into understanding the baffling variety of morphological diversity in larval fishes. Blackwater diving is defined as “epipelagic scuba dives conducted in relatively deep offshore areas after sunset” [1]. These dives enable in-situ observation, photography, and video of fishes and pelagic invertebrate taxa, with and without diel vertical migrations, in near-surface waters, undamaged by conventional collection techniques and handling. This method, albeit using artificial lights, allows us to present dramatic photographic evidence supporting the hypothesis of Greer et. al. (2016) [2] that the remarkable ontogenetic stages of some larval fishes represent a highly evolved survival strategy using Batesian mimicry to mimic gelatinous zooplankton in both specific and general ways, thereby reducing predation pressure and increasing survival.

We present here a selection of images to support this hypothesis designed around 4 primary themes:

1. The different categories of morphological adaptations used by larval fishes to increase their odds of survival.

2. Photographic evidence of the mortal hazards posed to larval fish by predators including gelatinous zooplankton.

3. Evidence of the potential effectiveness of gelatinous zooplankton mimicry inferred by illustrating protective commensalism behavior.

4. A gallery of examples illustrating putative Batesian mimicry of gelatinous zooplankton by a wide variety of larval fishes.

Materials and Methods

For a detailed description of blackwater diving, photography, and collecting see Nonaka et al. (2021) [3]. A majority of the photographs in this paper, taken by a variety of divers, including Richard Collins (RC), are from a single northwestern tropical Atlantic dive site off Palm Beach, Florida, USA. For details on the Palm Beach blackwater diving location and practice see Schuchert & Collins (2021, 2024) [4,5].

The photographs used for analysis here were mostly taken between 2016 and the present. Photographs from the Pacific and Indian Ocean were sourced directly from photographers, Instagram, Facebook, and other internet resources and were curated by G. David Johnson (GDJ). Photograph captions indicate photographer by their initials, following the list in Acknowledgments.

Most of the subjects were not collected for measurement or as voucher specimens – we are fortunate to just have the photographs! Plates do not show comparative images at the same scale. Some images were reoriented or reversed 180 degrees. Different photographers using different equipment and different post-production adjustments may introduce some photographic inconsistencies. We view these inconsistencies as of low importance, since the images are taken in bright, artificial lighting, while the actual environment that these creatures inhabit, especially the species that undergo diel vertical migrations, is a low-light environment.

Results and Discussion

The larval stage of most marine fishes is characterized by extremely high mortality rates, easily in excess of 90% [6]. Larvae are typically small (mm to cm) and vulnerable (i.e. limited escape and defense ability) and subject to three primary sources of mortality: limited food resources resulting in starvation and poor condition, predation, and drift to unsuitable locations for settlement. This paper is concerned with the second factor, predation. Avoidance of predation is of major importance to the early life stages of fishes. There are several ways this may be accomplished in pelagic waters:

1. Escape after detection by rapid swimming, evasion, or other behaviors.

2. Mechanical or gape-limiting defensive features such as protective spines on the head or fins are common features that can deter or thwart predation. Such structures act to limit the size of prey items that can be engulfed by a predator.

3. Non-detection (visual) by a predator due to color patterns (camouflage) or other visual cues. In this category, we include the relative invisibility conferred by transparency and/or visible features that serve to distract or confuse a potential predator.

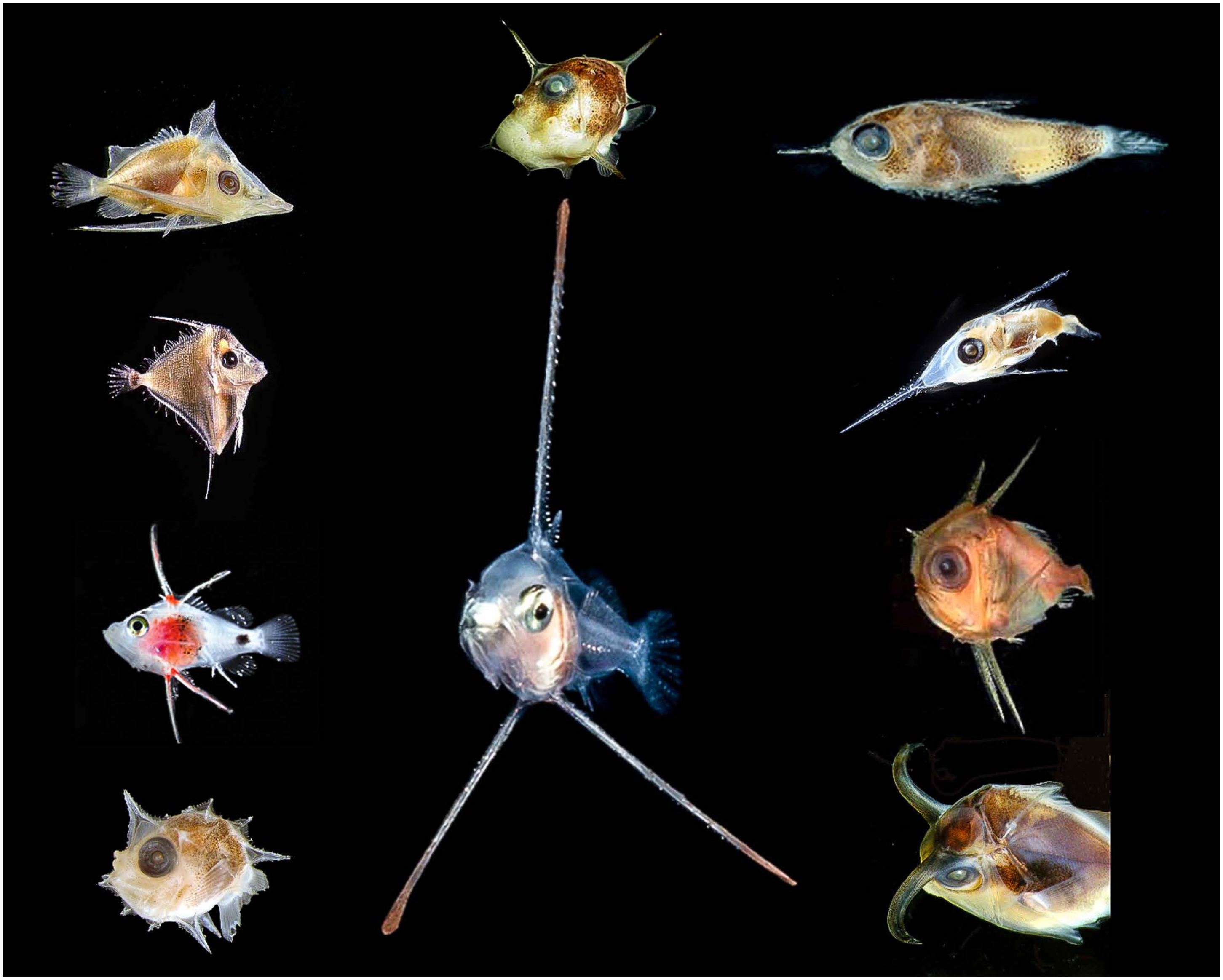


Figure 1. Extensive head and fin-ray spination offers mechanical predator deterrence: (clockwise from bottom left) fixed specimens of *Ranzania*, *Naso*, *Forcipiger*, *Hoplolatilus*, *Holocentrus*, *Anoplogaster*, and *Chaetodon* (all DJ), plus *Epinephelus*, live (at center) (LI).

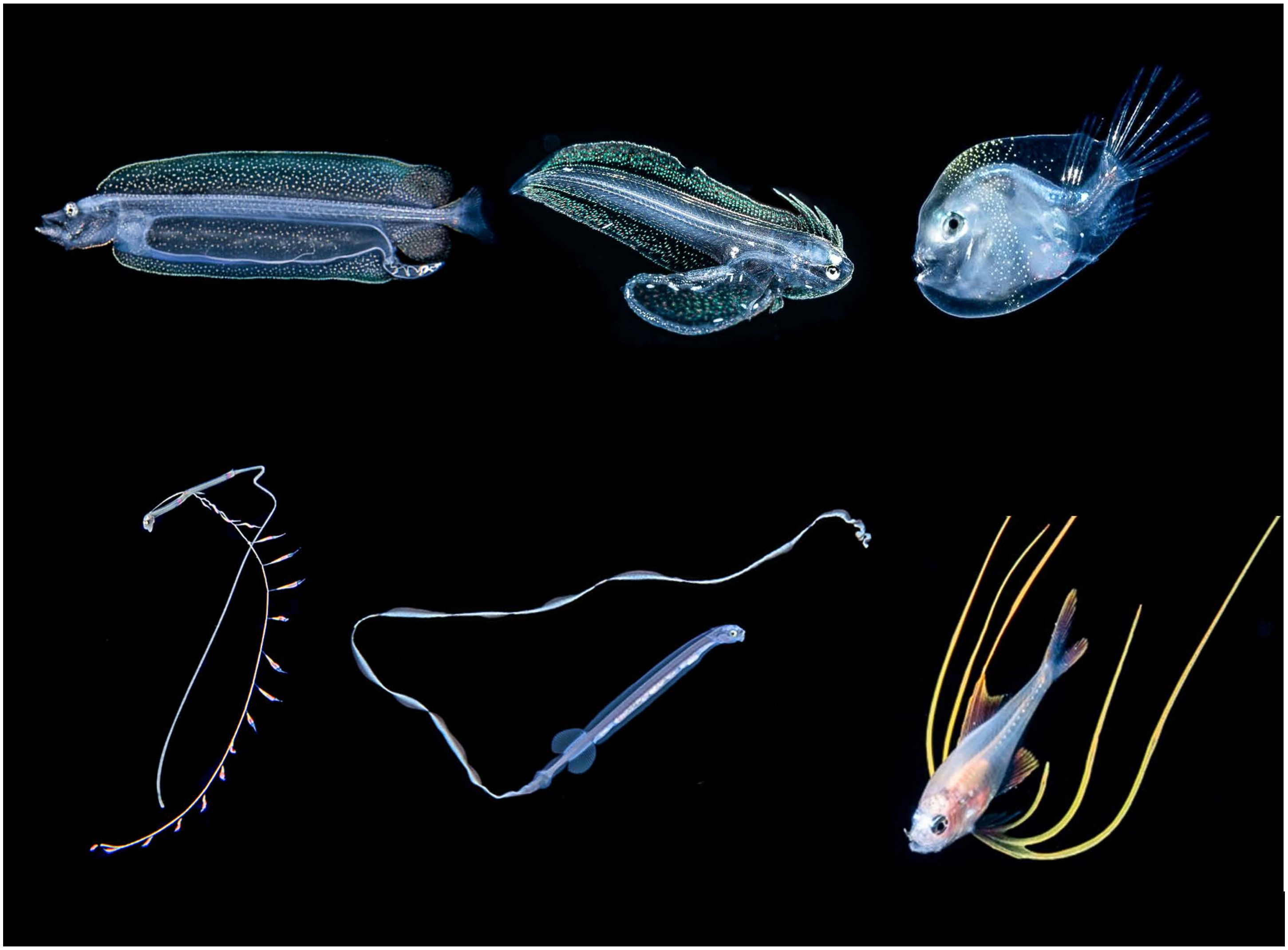


Figure 2. Soft tissue elaborations: (top row, left to right) fin folds in *Bathophilus* (LI), exterilium gut in Cynoglossidae (RC), and inflated sac in *Ceratias* (LI); (bottom row, left to right) elongate filamentous fin-ray extensions in *Carapus* (ND), *Gyrinomimus* (DD), and *Beryx* (LI).

4. A related form of non-detection might be behavioral, such as the association or "hiding" of larvae and pre-juveniles with either inanimate objects or living creatures. If a larva or pre-juvenile associates with a noxious or otherwise undesirable creature, then the hiding achieves an even more protective quality.

5. Diel vertical migration.

6. Advertising a similarity to abundant zooplankton that are unpalatable, dangerous, or otherwise avoided by predators, i.e. a form of mimicry can also be a way to avoid or reduce predation.

The last mechanism, Batesian mimicry, first proposed by Henry W. Bates (1862) [7], is the subject we will emphasize here, based on observations and photographs obtained by blackwater divers. Before expanding on that subject, further consideration of the second-listed mechanism, protective spination, will serve to illustrate the widespread occurrence of other extreme features that can be easily explained as simply structurally protective in nature.

Of the specialized features listed above, those with the most obvious function are the extensive armature of the head bones and spicule-like or keeled scales. Moser (1981) [8] explained the advantage of pungent head spines in terms of predator deterrence. In addition to fixed spines on many of the cranial bones, effectively increasing the head size, spines on the opercular series can be flared laterally, presenting a prey item that is effectively larger, painful, and/or dangerous to ingest, and thus more resistant to predation. As he noted in the paper "Such a protective effect may be enormous at the size range of fish larvae, where small increments in actual or apparent prey size may have a disproportionately large

Figure 3. Fin-ray elaborations at preflexion and flexion stages: (clockwise from bottom) *Acanthonus* (DW), *Cyclopsetta* (RC), *Trachipterus* (DD), *Monolene* (LI), *Barbourisia* (LI), and *Diploprion*, fixed (at center) (DJ).

effect in reducing predation by the smaller classes of organisms that prey on fish larvae". Pungent fin-ray spines play a similar role (Fig. 1).

Other specialized modifications are diverse and primarily involve modifications and extensions of soft tissues, voluminous fin folds, gelatinous body envelopes, elliptical or stalked eyes, elongate external extensions of the gut [8,9], and the elaborate, often highly ornamented, extensions of the fin rays that have repeatedly evolved independently in numerous unrelated taxa (Figs. 1, 2 & 3) Much has been speculated (but rarely tested) about the possible functions of these structures, with the recognition that they must come at a selective price in terms of active predator avoidance, i.e. they undoubtedly create varying levels of drag and thus inhibit rapid swimming and maneuvering. It is these simple to ornate structures that are the primary subject of our paper.

It is obvious that these embellishments must impose a disadvantage to the larval fishes that bear them since they restrict mobility for predator avoidance and make individuals obvious to predators, in a sense, "advertising themselves". Strengthening this premise is the fact that many of these structures appear in early preflexion and flexion individuals, when locomotory abilities are not fully developed (Fig. 3).

Accordingly, it seems reasonable that there must be some counteracting selective advantage. One explanation may be that elaborate and/or voluminous fin rays are another application of Moser's (1981) observation about small increments in actual or apparent prey size having a disproportionately large effect in reducing predation by the smaller classes of organisms that prey on fish larvae [8]. With the large number of blackwater photographs at our disposal, another now obvious potential explanation for this combination of properties is Batesian mimicry of predatory, unpalatable, or nutritionally deficient organisms in the plankton (e.g. gelatinous zooplankton with high-water, low-carbon content [10].

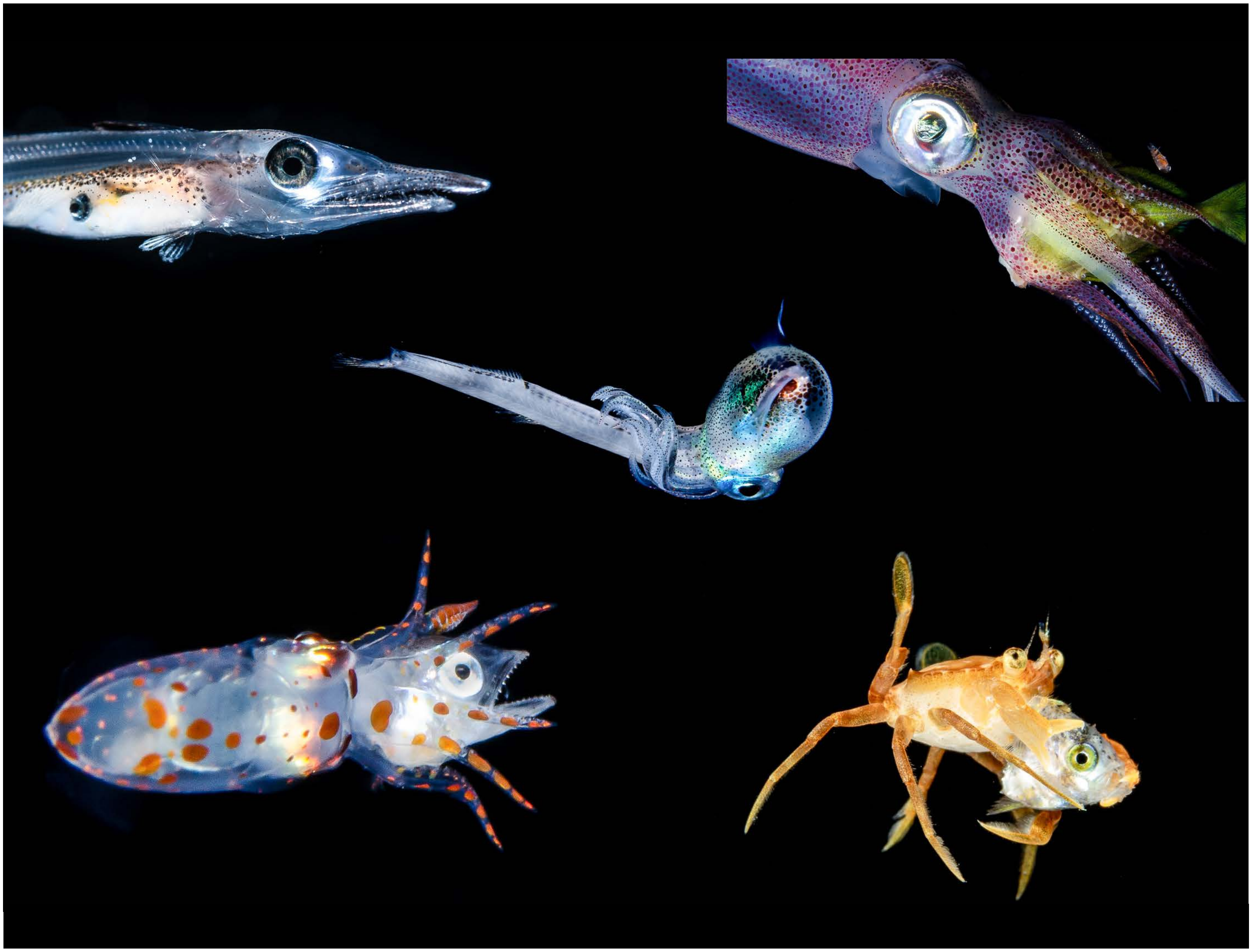


Figure 4. Predation on larval fishes by visual predators: (clockwise from lower left) paralarval squid (DD), *Acanthocybium solandri* (RC), squid (DD), sargassum swimming crab *Portunus sayi* (SM), and paralarval squid (at center) (DD).

In other words, they are visual warning signals that larva should be avoided by predators.

Until recently, with the exception of Greer et al. [2], the possibility of mimicry by larval fishes in the plankton has received little attention, aside from a few cursory observations of resemblance to siphonophores or hydromedusae tentacles by certain elaborately ornamented fish larvae [2,8,11–14], and, most recently, Miller's (2023) [15] consideration of eel leptocephali, emphasizing transparency and pigmentation. According to Govoni et al. (1982) [13] "five hypotheses on the function of elongate dorsal appendages among larval teleosts are that they serve in sensory perception [8,16], camouflage or predator deception [8], protection or predator deflection [8,16], flotation [11,17–19] and prey attraction [8]. Among these hypothesized functions, flotation predominates."

Although the hypothesis of Batesian mimicry had been proposed before, the real breakthrough in our understanding of form and function in many of the larval forms under discussion came with the seminal paper of Greer et. al (2016) [2], who, for the first time, addressed the likelihood of widespread Batesian mimicry by larvae of marine fishes and discussed three necessary conditions for Batesian mimicry:

1. Visual predation must be a strong source of mortality. Predators inflict a heavy toll on the young stages of fishes and probably are the single greatest cause of mortality (can be greater than 99% during the egg and larval stages [6]) (Figs. 4 & 5).

Figure 5. Unidentified larval fishes captured by various gelatinous zooplankton: (clockwise from bottom left) siphonophore (RC), *Liriope tetraphylla* (RC), *Liriope tetraphylla* (RC), *Geryonia proboscidalis* (LI), and gempylid captured by *Athorybia rosacea* (SK) (gempylids are predators of larval fishes).

2. There is a relatively abundant and unpalatable (or undesirable) model that the mimic resembles. Small gelatinous zooplankton are extremely abundant [20,22] with high water content, relatively low carbon content [10], and many have stinging nematocysts or entangling sticky filaments, making them effective predators to be avoided (Fig. 5).

3. Mimicry must provide an umbrella of protection, whereby mimics with only a slight resemblance to a model or models receive some degree of protection. This is paramount because the vast variety of zooplanktonic life is distributed over very large areas, and, except for blooms, is at low density. This means that overly specific mimicry, without the same defenses as the modeled gelatinous zooplankton (e.g. nematocysts), and with the associated liabilities of mimicry (e.g. decreased speed and mobility), would be ineffective. Furthermore, the strategy would limit the geographical, depth, and environmental profile of the mimic to that of the model. If the model's range or viability was reduced or eliminated due to changing environmental factors, then the associated mimic would face decreased range and or increased predation pressure. Furthermore, it seems reasonable to assume that the anatomy of fishes generally restricts the degree that exact duplication of gelatinous zooplankton is possible.

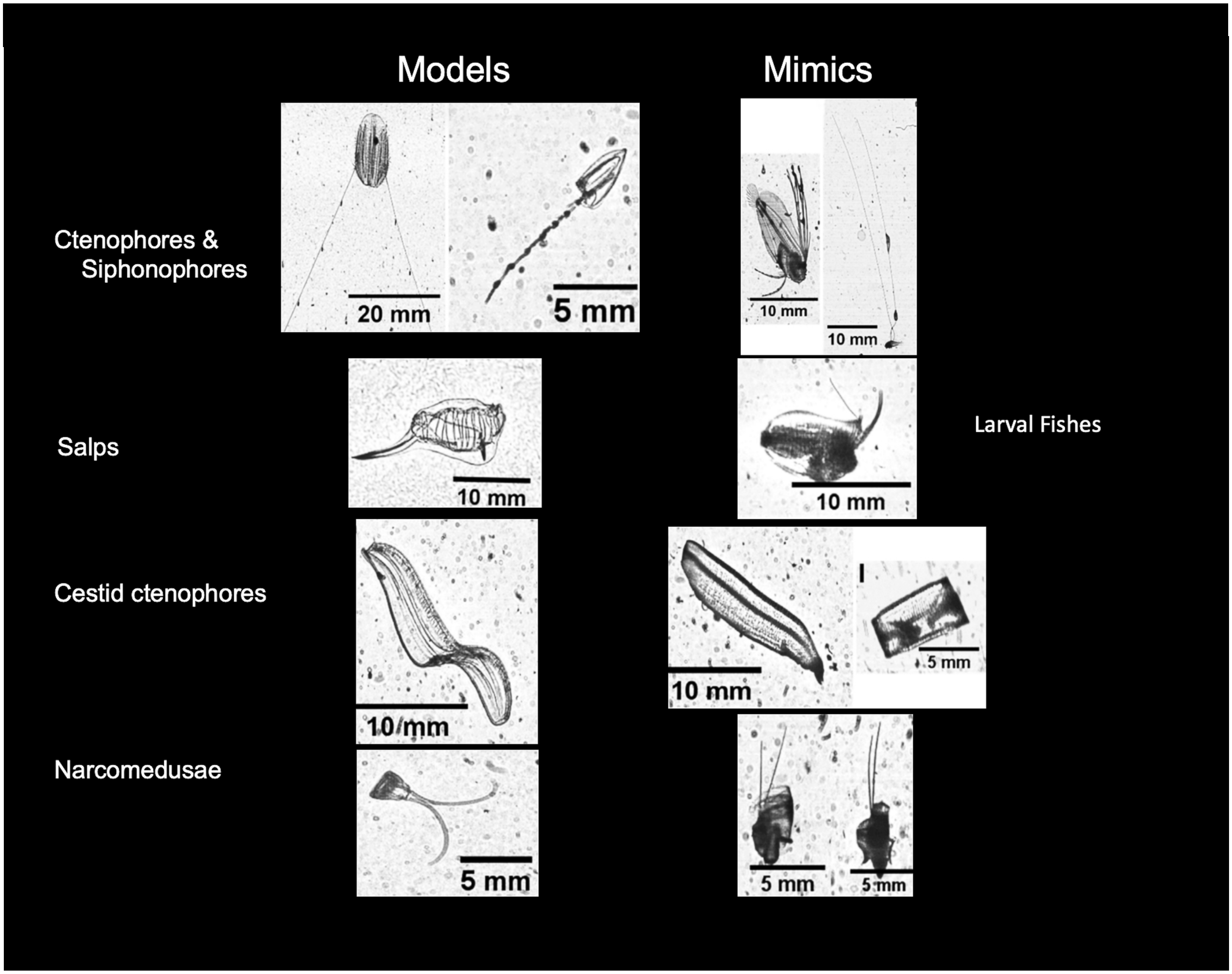


Figure 6. Mimics and models from Greer et al. (2016) showing shadowgraphs taken with ISIIS (In Situ Ichthyoplankton Imaging System), CC-BY, used here with permission of the author.

Greer et. al. (2016) used a mathematical model designed to show that complex and metabolically costly traits can spread through and dominate in a population relatively quickly (evolutionary time would represent thousands of generations), even with only a miniscule advantage for larval fish survival [2]. We accept the evidence presented by Greer et. al supporting the hypothesis that "Batesian mimicry could be a common survival strategy for larval fishes", and our intention here is to bring another visual perspective to it with a much more diverse suite of in-situ images [2]. Greer et. al. collected images of larval fishes and their zooplankton models for mimicry using the In Situ Ichthyoplankton Imaging System (ISIIS) (Fig. 6) [2,23]. Among the advantages of this method is that it allows quantitative recording of large numbers of organisms with a relatively standardized light regime and physical perspective. A significant disadvantage is the fact that all images are shadowgraphs, which lack the color and surface details provided by live in-situ images and diver observations.

With the recent popularity of blackwater photography, and the availability of thousands of images, it occurred to us that these in-situ images of larval fishes and gelatinous zooplankton could provide an enlightening perspective on mimicry in the plankton. It is with that goal that we offer these comparative images and discussion (Fig. 7).

As reviewed by Greer et. al. (2016), there is extensive literature about crypsis and camouflage in the open ocean [2]. Johnsen (2014) noted "Transparency is the simplest form of pelagic camouflage – because the underlying principle is intuitive (i.e., invisibility) and complex because the morphological and physiological mechanisms underlying it are poorly understood." (Fig. 8) [24].

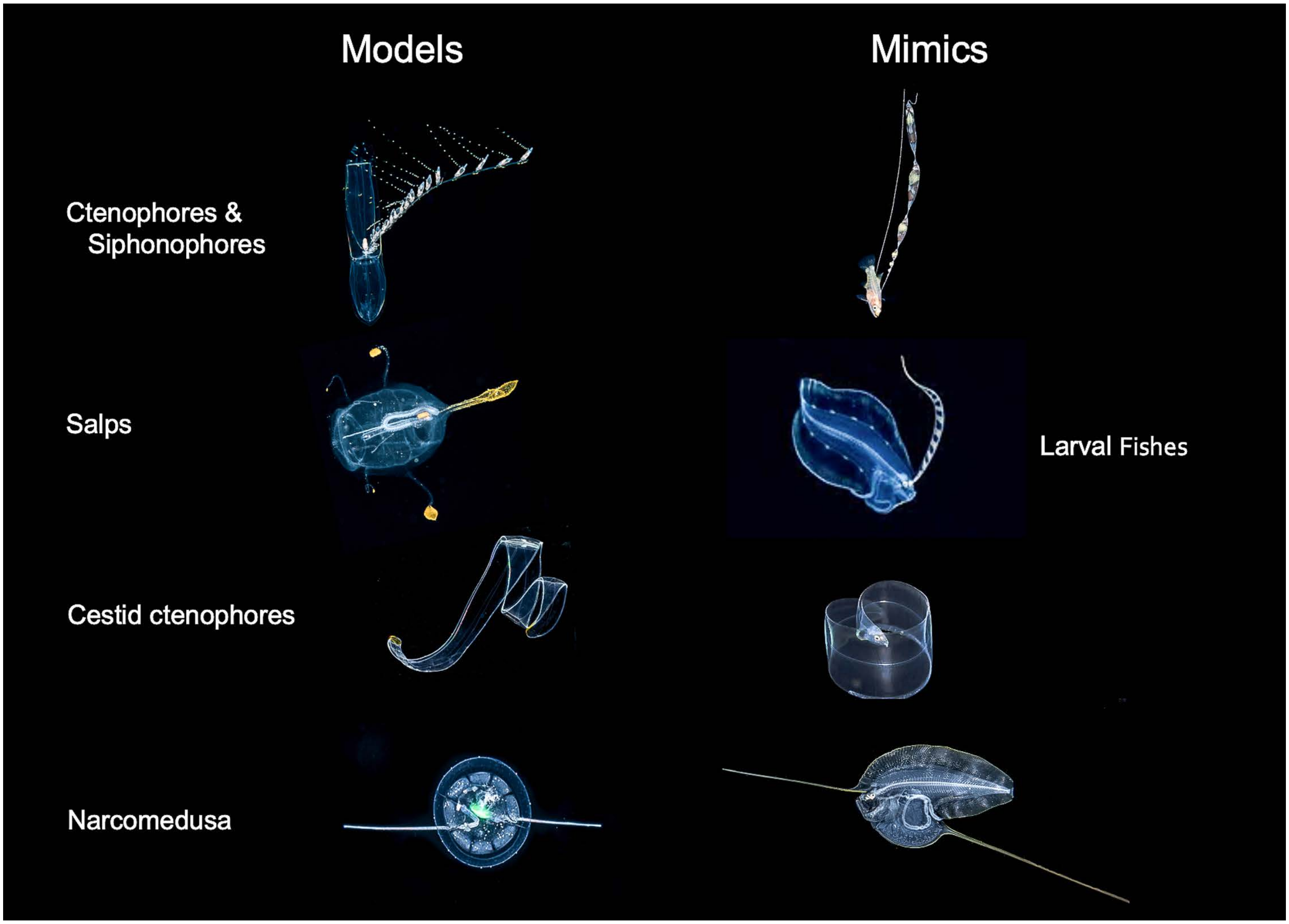


Figure 7. Mimics and models based on Greer et al (2016) with live blackwater images substituted: see other figures for photographer credits, except the salp (AW).

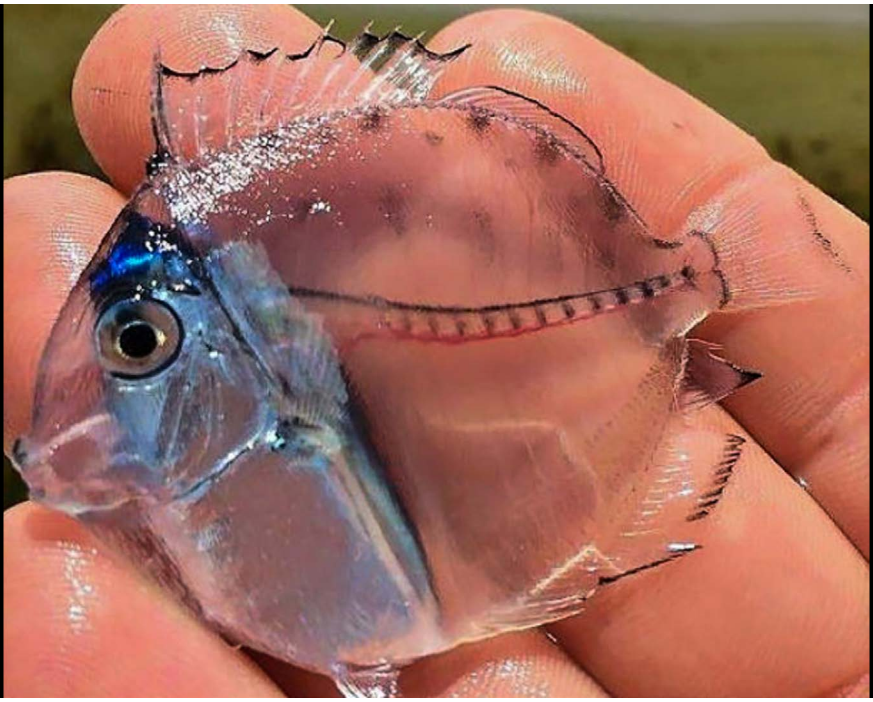


Figure 8. Larval acanthurid (KM), demonstrating transparency, seen most easily when out of water.

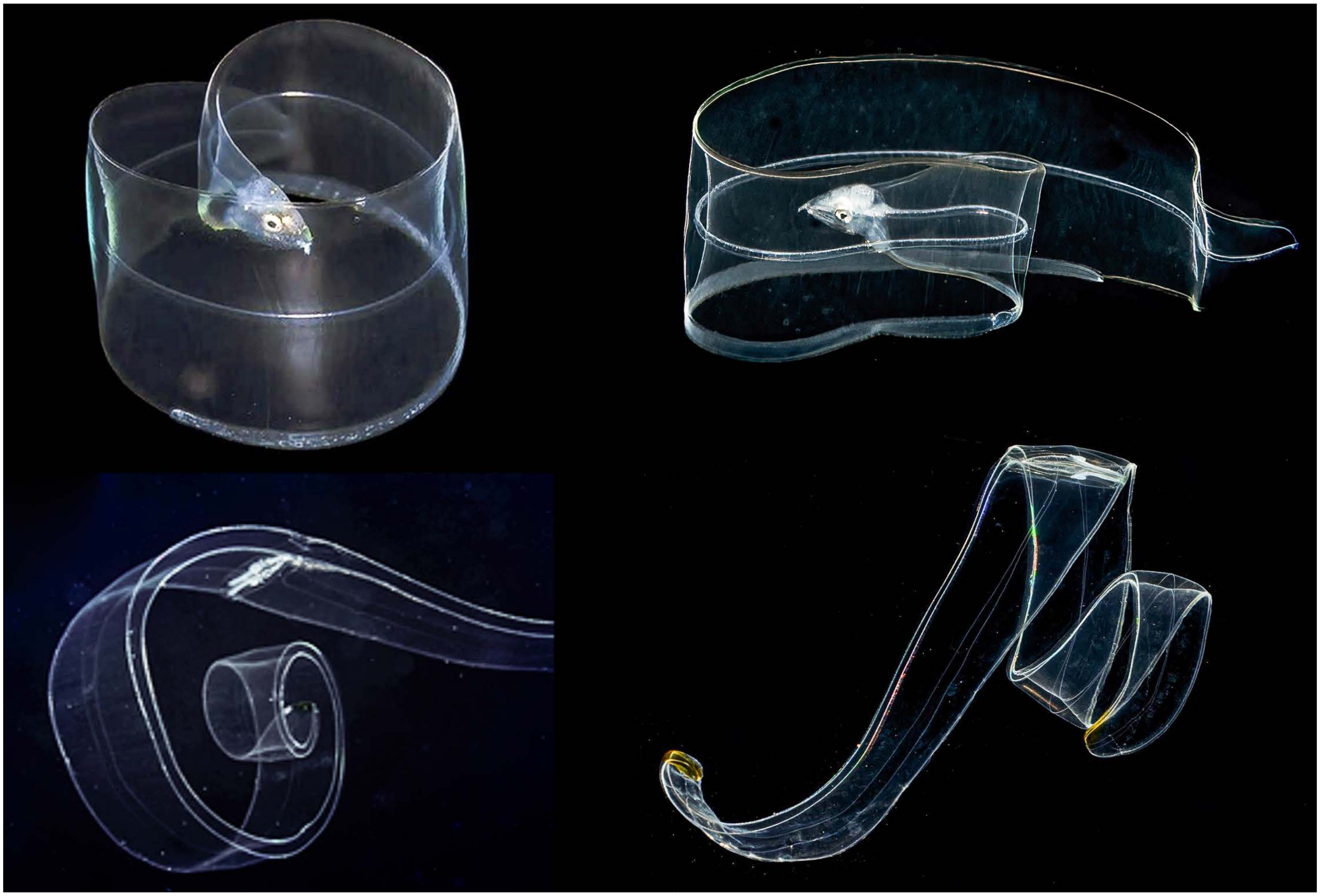


Figure 9. Putative mimicry: leptocephali (upper pair) (SK); Venus girdles, cestid ctenophores (lower pair) (RM left, SM right).

As documented recently, perhaps the masters of transparency among larval fishes are the leptocephalus larvae of true eels (Anguilliformes) and other elopomorphs, and their resemblance to the undoubtedly less-nutritious cestid ctenophores, e.g. *Velamen parallelum*, has often been noted [15] (Fig. 9).

Nonetheless, total transparency is rare among larval fishes. Even the almost totally transparent leptocephali may have a few pigment spots, some of which are expandable [15]. Most fish larvae have varying degrees of pigmentation, and it often appears to be placed in ways that could be seen as facilitating predator deception. For example, as discussed by Moser (1981), some animals (e.g. snakes) have repeated "elements" along their vector of motion, and it has been proposed that this could result in "flicker fusion," an effect that could help prevent capture by confusing predators, and thereby reducing the chances of initial detection of the prey [25]. This could be the case for the larvae of some aulopiforms (particularly lizardfishes) and some leptocephali, which have repeated black or yellow ventral-midline spots (respectively). Certain reflective pigment placement can also lead to misdirection of the predator, wherein larvae with reflective guanine pigmentation surrounding their viscera can possibly give the impression that the prey is moving in a different direction (Fig. 10).

In many cases, transparency appears to facilitate visual emphasis on other opaque and/or reflective structures that may be involved in mimicry (Figs. 11a & b), wherein individuals are shown with and without their fin-ray embellishments occluded.

Mimicry Matches

As we have discussed, an intriguing feature of many, if not most, pelagic larval fishes are that transparency of the body is combined with pigmented markings, and, in particular, the pigmented features may also occur as swellings and other decorations on filamentous fin rays or other extensions from the body. Immediately the question arises – why

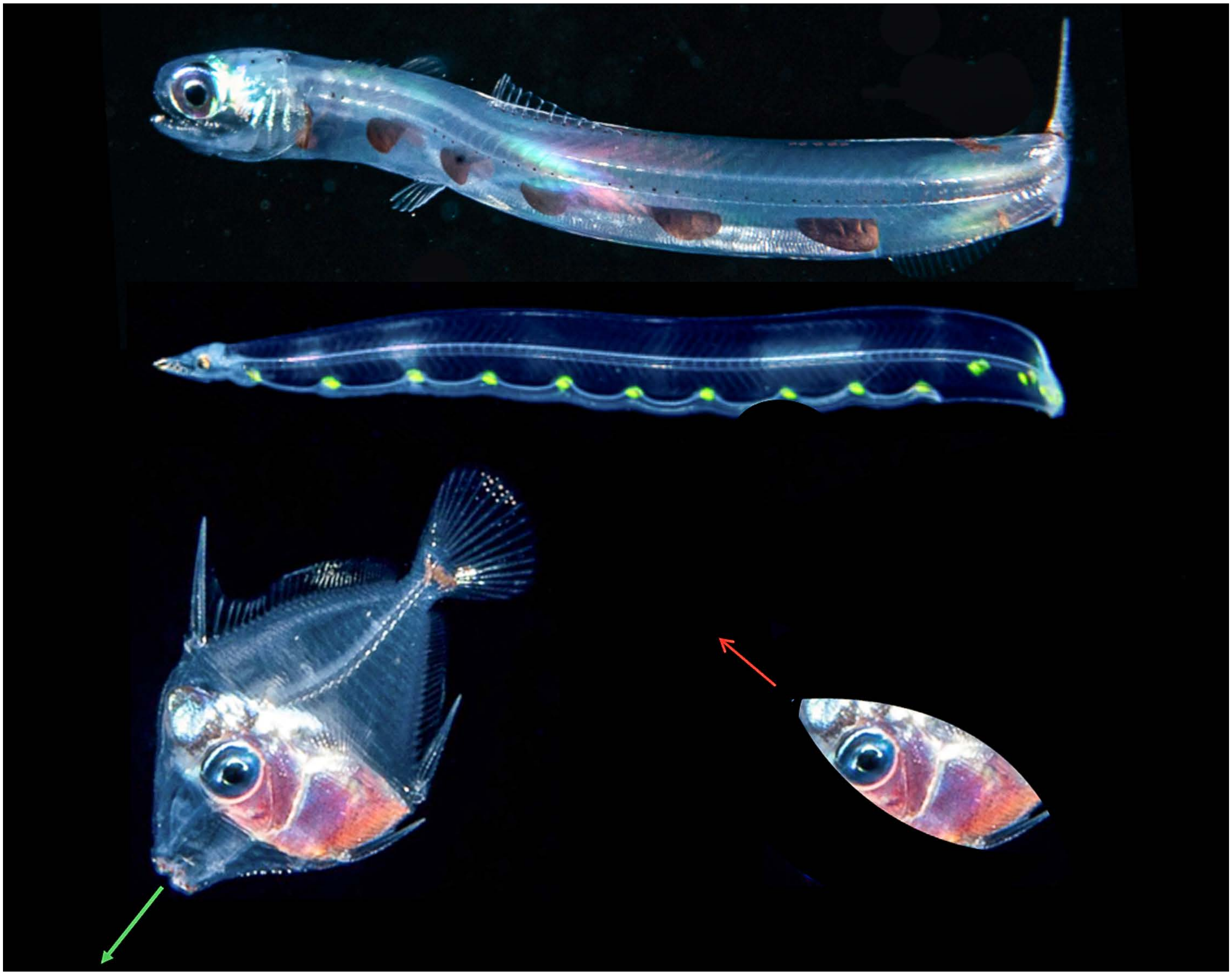


Figure 10. Potential flicker fusion: *Trachinocephalus* (top) (LI); Ophichthidae (middle) (LI). Potential misdirection: (lower pair) *Acanthurus* (LI) entire at left and same specimen, transparency occluded (arrows indicate possible perceived direction of swimming).

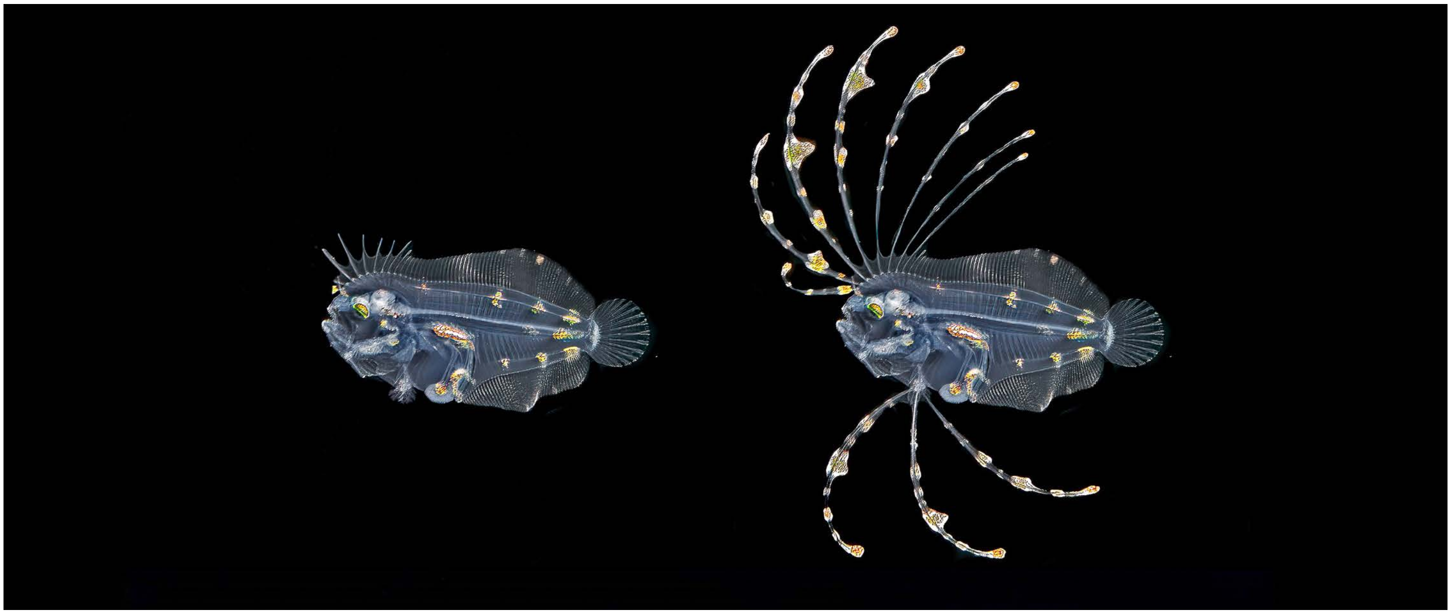


Figure 11a. Fin-ray elaborations: *Cyclopsetta* (occluded left and visible right) (ND), filamentous fin-ray extensions removed digitally.

Figure 11b. Fin-ray elaborations: *Liopropoma* (occluded left and visible right) (WS), filamentous fin-ray extensions removed digitally.

would larvae have a feature that minimizes communication (transparency) but also have markings and anatomical features that appear to maximize communication or even draw attention to the presence of the larva to visually hunting predators? Until recently our knowledge of these structures was most frequently based on net-collected specimens, which have often suffered from net abrasion and fixation artifacts.

Based on the less-than-optimal, net-collected, and preserved specimens, various functions for these poorly known elements have been suggested.

Possible other functions for soft-tissue elaborations:

1. **Buoyancy**. It has often been hypothesized that the increased surface area created by these structures could generate drag that would prevent sinking of the individual or even serve as flotation devices [8]. Blackwater video of several different ornamented larval fishes (e.g. *Liopropoma* and *Carapus*) demonstrates that they swim independently of these structures and do not depend on them for maintaining position in the water column. Furthermore, most larval fishes have well developed swim bladders that facilitate vertical migration, so there is no need for buoyancy assistance. Exceptions may be the inflated surrounding sacs of larval lophiiforms and some tetraodontiforms, most of which lack a swim bladder. It is conceivable that the inflated sacs of lophiiforms and some tetraodontiforms assist osmotic buoyancy by physiological control of osmotic concentration in the same way that fish eggs achieve buoyancy by internal control of their specific gravity [26].

2. **Prey attraction**. Despite some speculation about this subject, there is no dietary or behavioral evidence that these structures act as lures to attract prey.

3. **Sensory detection of prey or predator**. There is no conclusive histological or behavioral evidence for a sensory function (but see Govoni et al. (1984) [13] for a possible exception in carapids).

4. **Toxicity**. There is no conclusive histological or behavioral evidence that these structures are noxious in any way.

There are perhaps other possible functions of these structures, but, whatever those may be, it is critical to remember that the visibility of individuals to predators is clearly facilitated or emphasized – they are advertising themselves, and therein we come to Batesian mimicry, the phenomenon we believe offers the most convincing reason for their existence. This is where the value of blackwater observations and photographs has added a new set of data on both the living appearance of larval fishes and other organisms in their environment. These data are the basis for our interpretation of the functional significance of various extraordinary larval-fish features.

As we present these various model/mimic scenarios, we acknowledge that the planktonic realm is complex, highly dynamic, and poorly understood in terms of physical and behavioral parameters. Accordingly, we note the following caveats:

1. Our evidence is all from the perspective of the human eye and brain in viewing photographs. Photographs also have an inherent bias with respect to spectral sensitivity. Importantly, there is little information concerning predator vision and search patterns.
2. Blackwater images are from the epipelagic zone, taken at night with artificial lighting. There is very limited information about transparency, reflectivity, and color in low ambient light, which varies with depth, moonlight, cloud cover, water clarity, and other factors.
3. Blackwater photographers are keen on capturing the most engaging and least ambiguous images. Accordingly, the most common published photographic point of view is lateral, while predators see or sense their prey from various perspectives. We do not believe this is a critical issue since non-lateral perspectives are often even more ambiguous and would seem to increase uncertainty for the predator. Additionally, blackwater divers tend to photograph the large and more unusual or spectacular fish larvae, and smaller simpler larvae are possibly underrepresented. There's also a question of the relative abundance of these larvae further offshore and at the depths where most blackwater dives occur.
4. Behavioral information is limited. Although images of live specimens are far superior to the previous alternatives, behavioral observations are few and far between. Unfortunately, dive lights and photographic illumination most likely affect typical in-situ behavior
5. The many composite photograph figures used to compare fishes with putative invertebrate mimicry models do not have scale bars to illustrate actual sizes. The source photographs were obtained by different blackwater photographers. Almost all organisms were between 0.5 and 5 cm in length or diameter, and thus of comparable size as illustrated in the

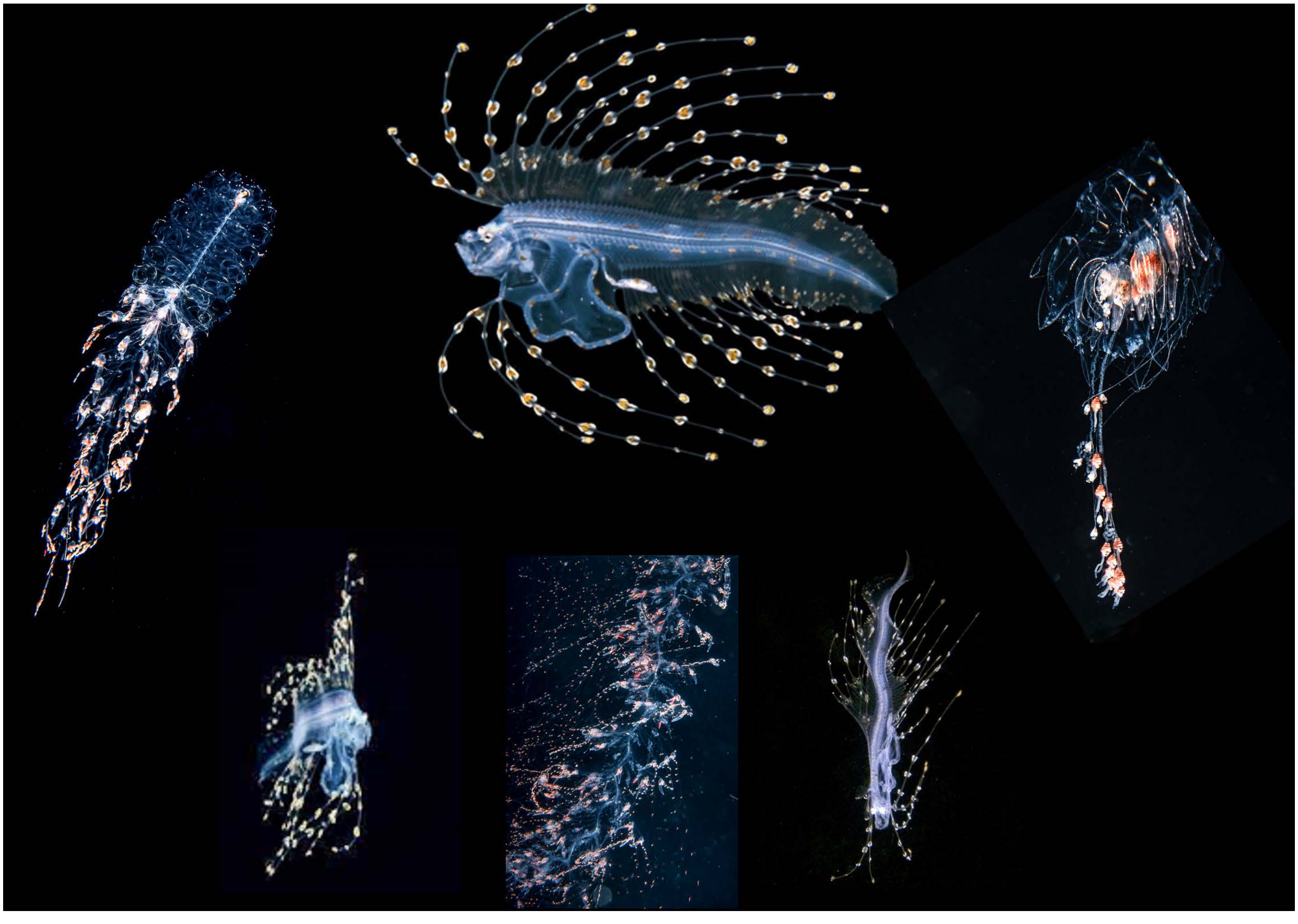


Figure 12. Putative mimicry by *Brotulotaenia* of siphonophores: (clockwise from lower left) *Brotulotaenia* frontal view (LI), siphonophore *Forskalia edwardsii* (RC), *Brotulotaenia* lateral view (SK), siphonophore *Agalma clausi* (RC), *Brotulotaenia* dorsal view (MD).

figures. Actual size is somewhat irrelevant for determining similarity since potential predators may view the models and mimics at varying distances and with variable visual acuity. Furthermore, consistent with Greer's necessary conditions for Batesian mimicry, mimics with only a slight degree of resemblance receive some degree of protection [2,27]. What is perhaps most important is that the mimics and models are found in the same environment at the same time.

The following plates offer what we believe to be reasonable mimic and model matches that could serve to deceive predators and discourage predation (Figs. 12–33). The figures are not accompanied by additional text because the legend texts convey the relevant mimicry potential. As the reader peruses these comparative images keep in mind that Greer et al. (2016) noted that mimics with only a slight resemblance to a model or models receive some degree of protection [2]. Sherratt (2002) investigated imperfect resemblances between Batesian mimics and their models using a quantitative simulation and found that factors such as the cost of attacking the model, the difficulty of capturing the mimic, degrees of sympatry, and the relative abundances of the model and mimic all had effects on the results. His model predicted that under some common conditions "the optimal phenotype should be a 'jack-of-all-trades' intermediate phenotype that does not closely resemble any particular model species." [27]. In considering Sherratt's conclusion it occurred to us that there is another factor that's usually not addressed because many of the Batesian mimicry studies involve birds (with highly acute vision) feeding in daylight. The blackwater-environment predators likely have lower acuity vision and they are feeding on moving targets in a low light, three-dimensional environment where prey may be encountered in any orientation. These circumstances would also be expected to have a significant effect on the level of resemblance required for effective mimicry [24].

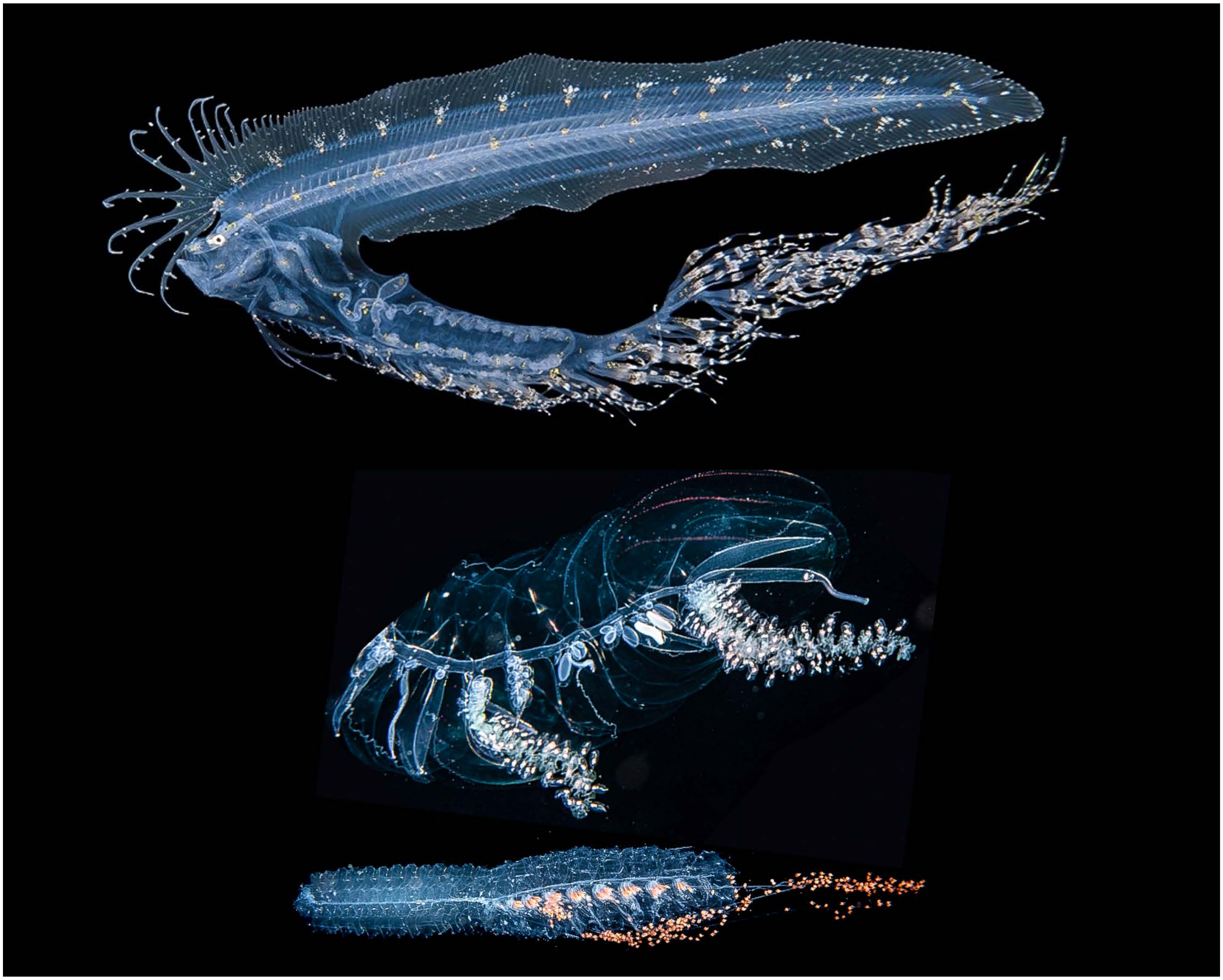


Figure 13. Putative mimicry by *Lamprogrammus* (top) (SK) (relevant ornamentation is borne on the exterilium gut that characterizes some cusk eels) of two *Agalma* spp. siphonophores (lower) (RC).

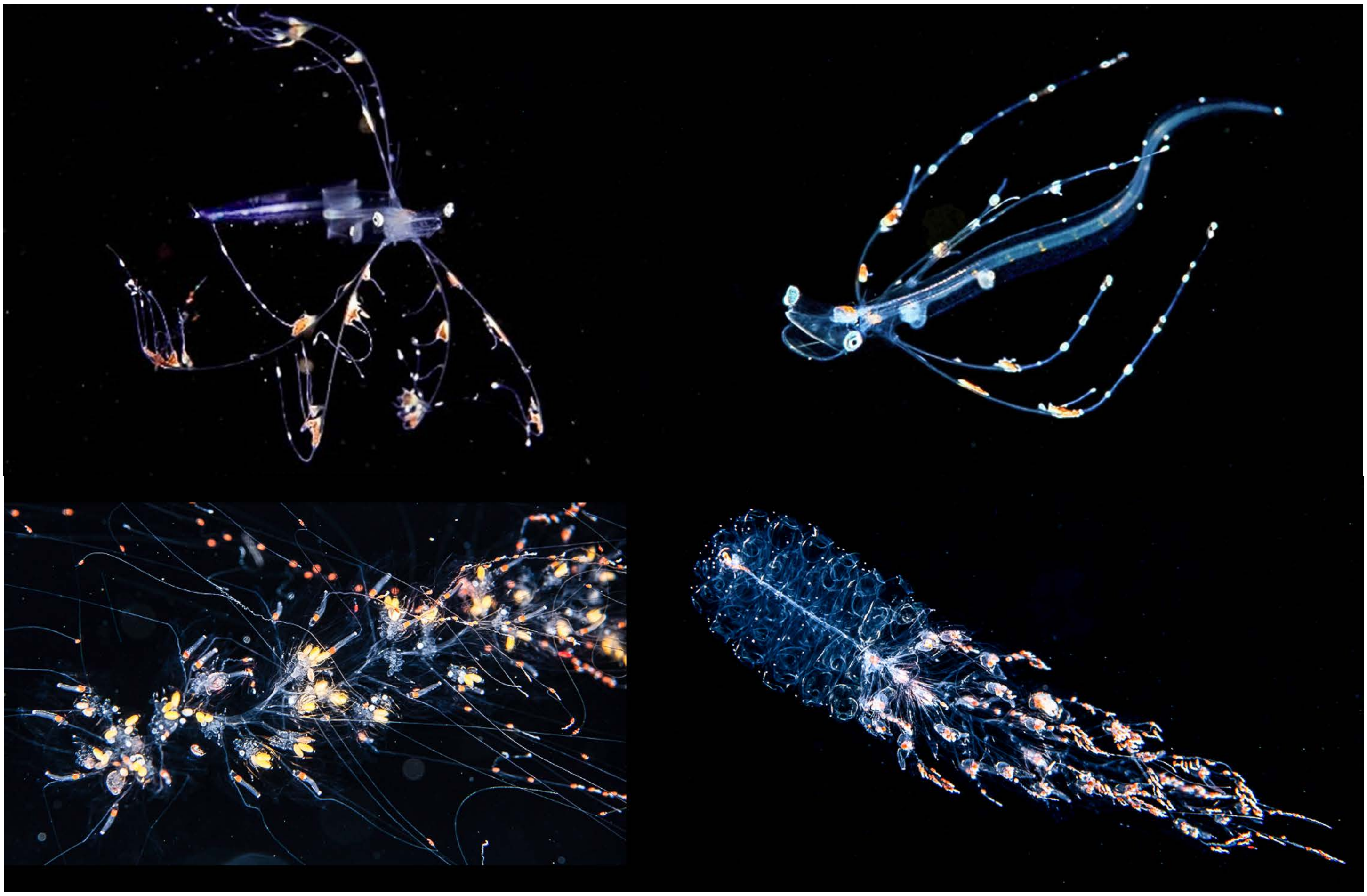


Figure 14. Putative mimicry by ateleopodid larvae (top left) (EY), (top right) (DC) of two siphonophores (lower) (RC).

Figure 15. Putative mimicry by *Gibberichthys* (center) (MO), of scyphozoan *Mastigias papua* (left), and hydrozoan *Pandeopsis* (right) (LI). *Mastigias papua* image by Adrian (User:Intandem) at en.wikipedia, CC-BY-SA-3.0, released under the GNU Free Documentation License (original image is cropped).

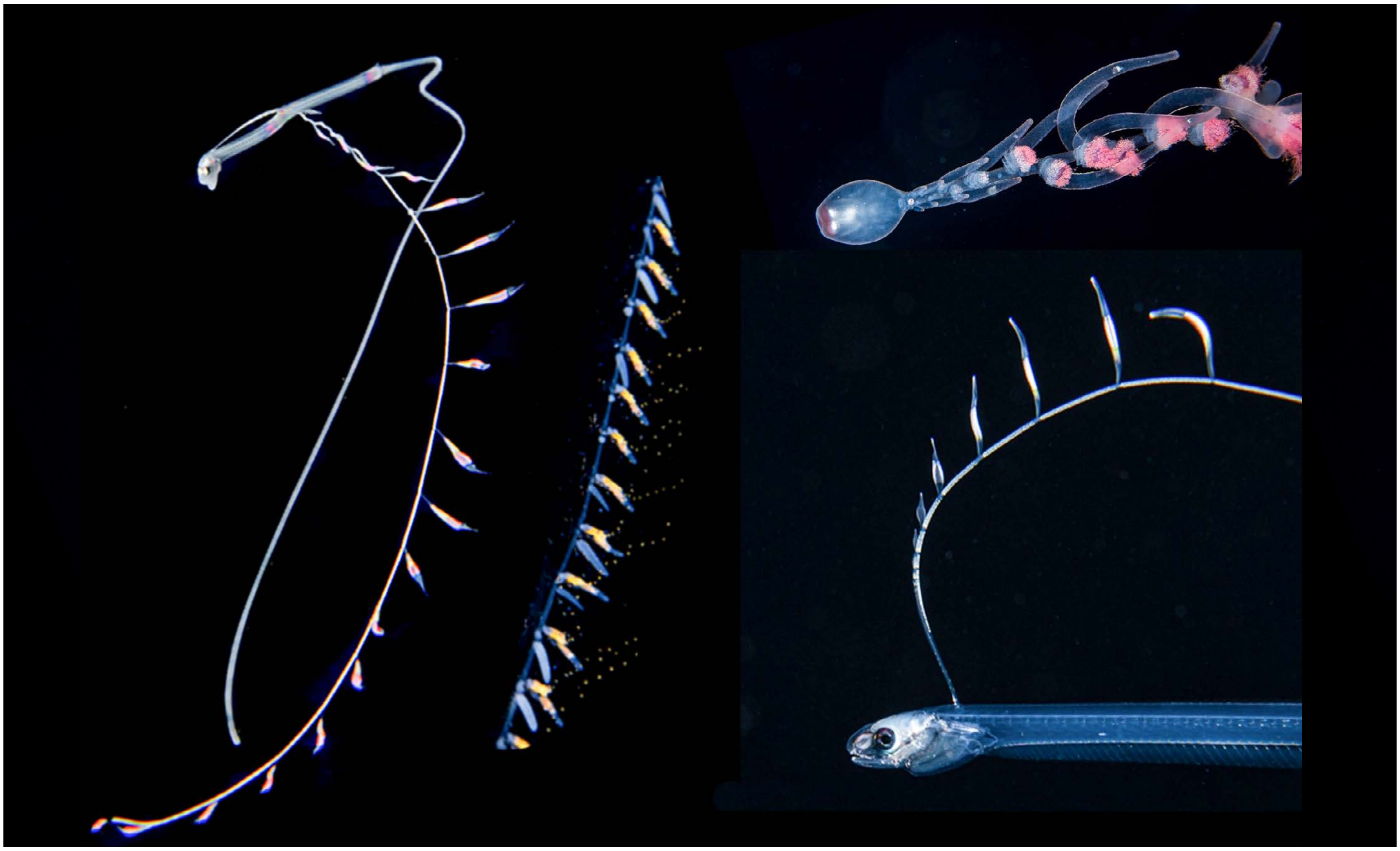


Figure 16. Putative mimicry by *Carapus* (left) (ND) (lower right) (RC), with stalks with bangles, of gastrozooids of siphonophores (middle) (MB), *Rhizophysa* (upper right) (RC).

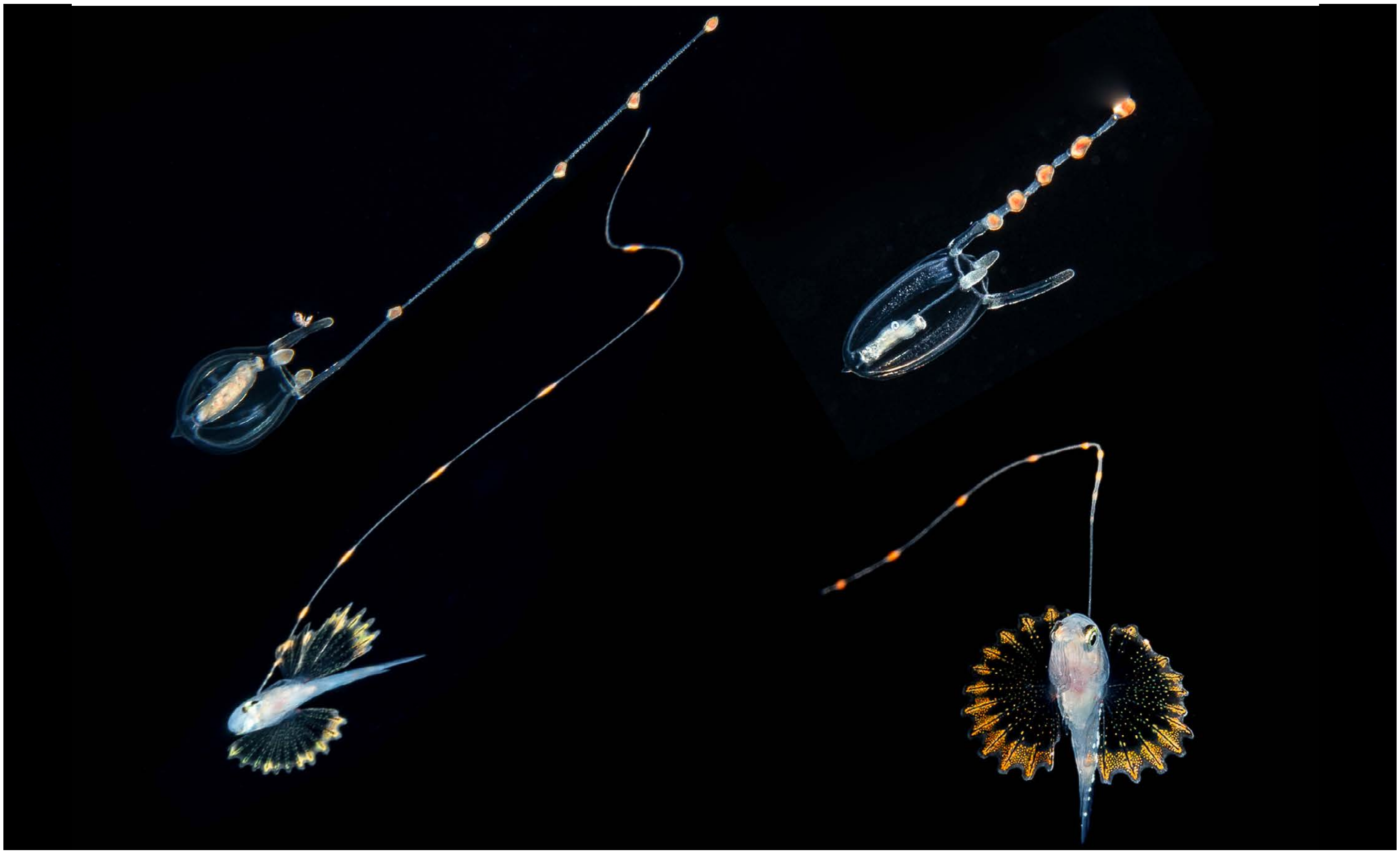


Figure 17. Putative mimicry by *Rypticus* (lower pair) (LI), with stalks with small swellings, of hydrozoans *Corymorpha floridana* (upper pair) (RC).

Figure 18. Putative mimicry by *Monolene* (left pair) (LI) of pelagic nudibranch *Phylliroe lichtensteinii* (upper right) (RC) and hydrozoans *Corymorpha forbesii* (center) (RC) and *Corymorpha gracilis* (lower right) (LI).

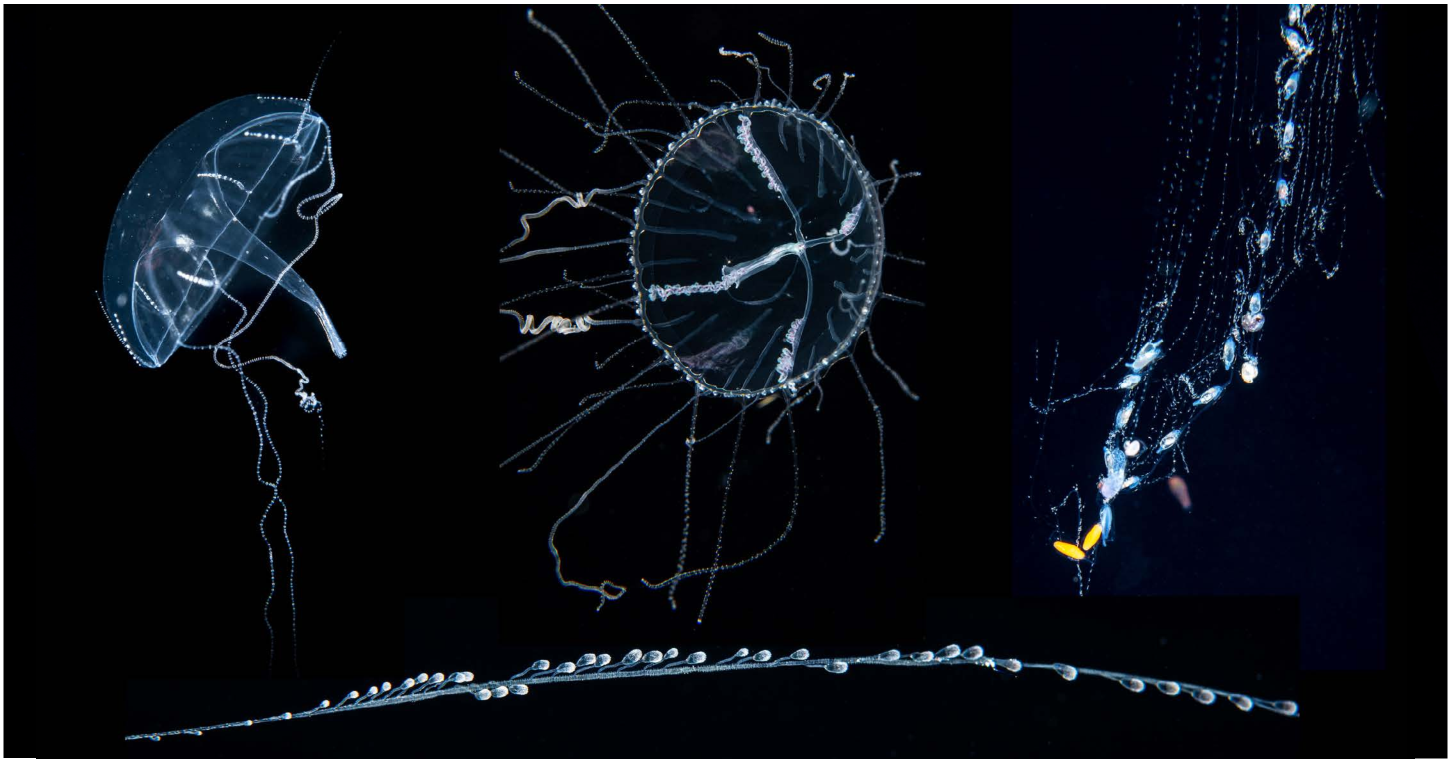


Figure 19. Putative mimicry by many larval fishes with elongate fin rays which closely resemble tentacles of various cnidaria showing small notches, bands, or bulbs that represent cormidia or nematocyst batteries: (clockwise from upper left) Limnomedusae *Geryonia proboscidalis*, *Olindias tenuis*, Calycophorae siphonophore, and Anthomedusae *Zancleopsis cabela* (all RC).

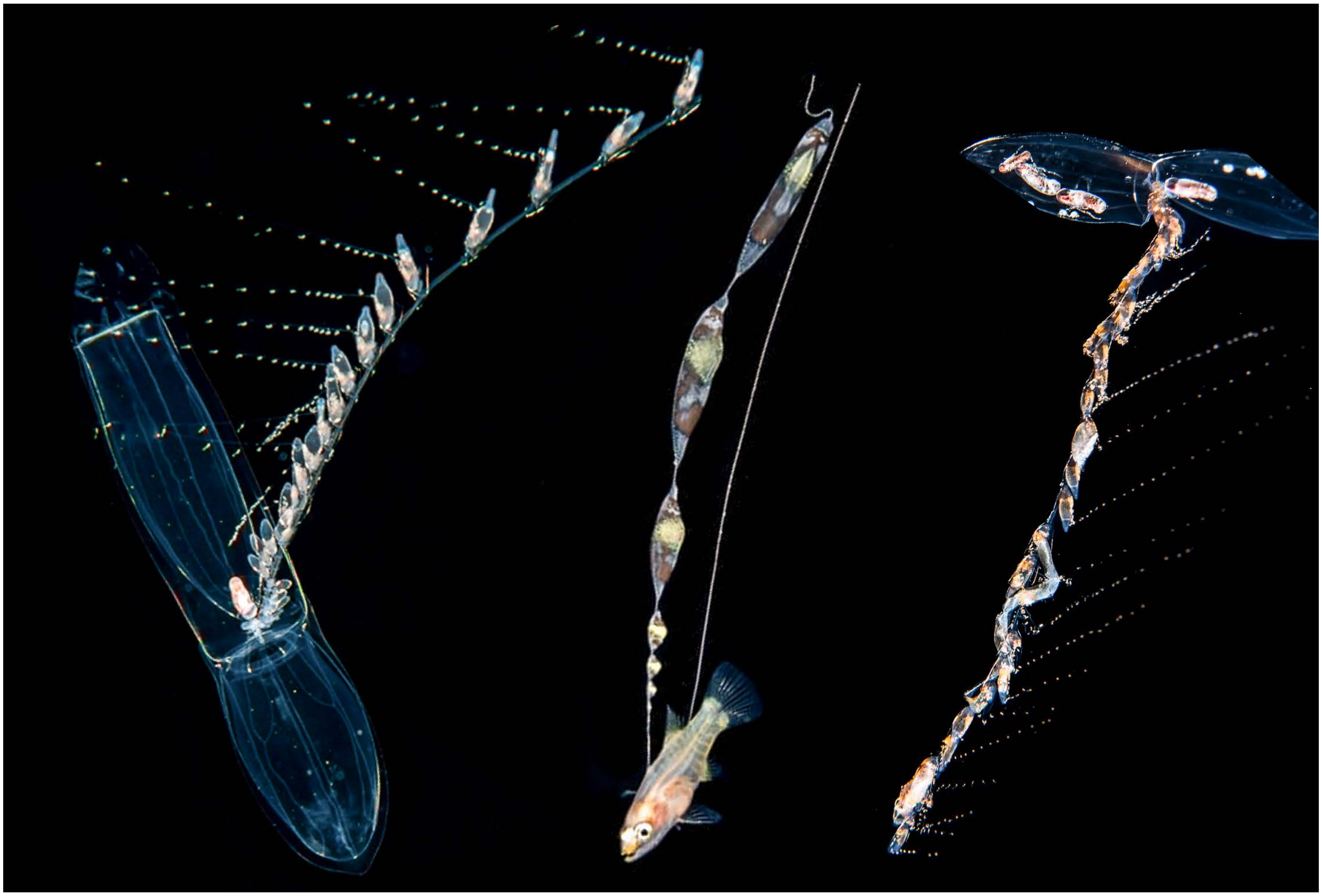


Figure 20. Putative mimicry by *Liopropoma* with ornamentation of the elongate first dorsal-fin spine (center) (SM) of siphonophores of Calycophorae (left and right) (RC).

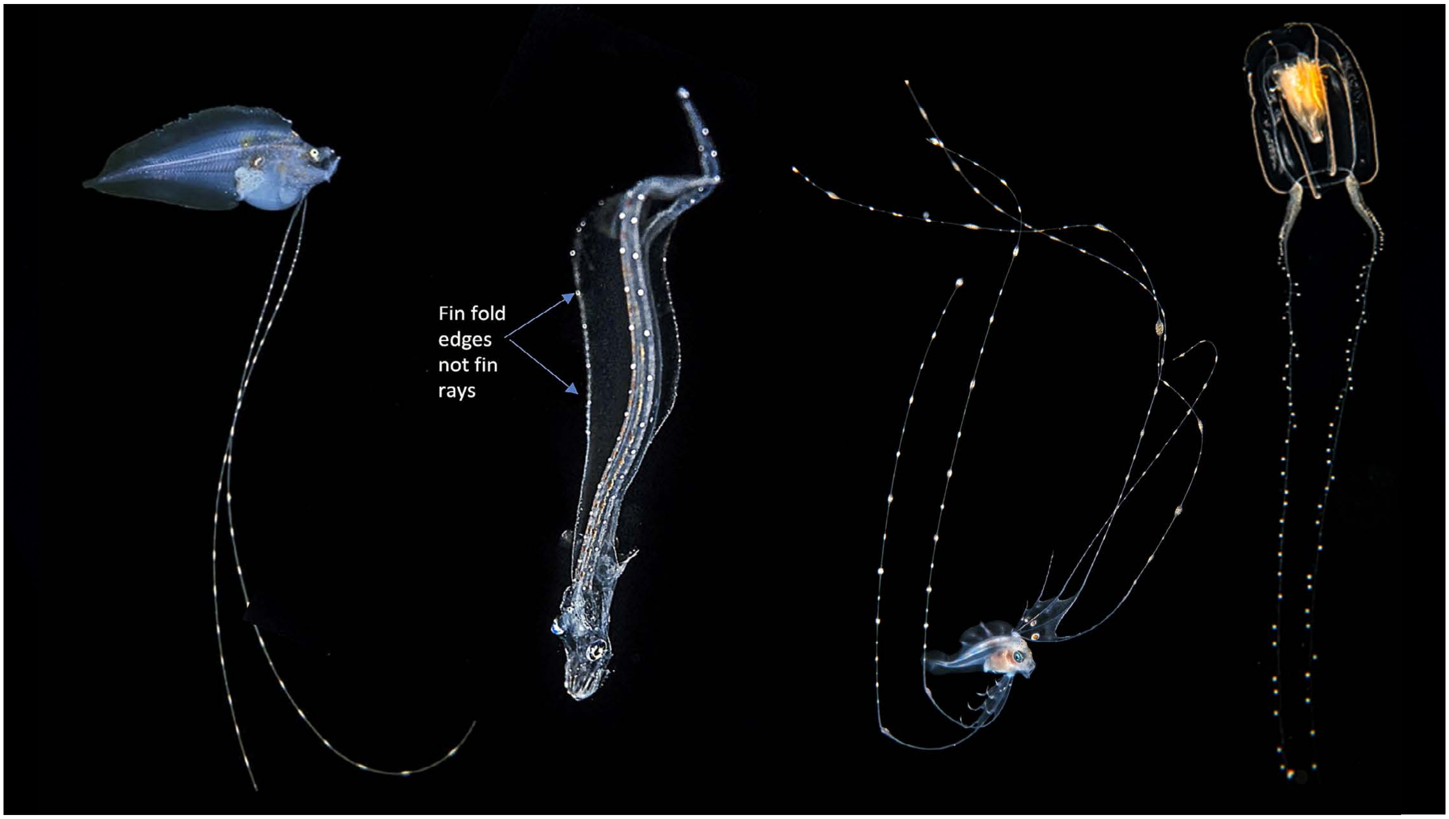


Figure 21. Putative mimicry by fishes of nematocyst-bearing tentacles (also see Fig. 22): unknown bythitoid (left), stomiid (left center), and *Trachipterus* (right center) (all SK), compared to the hydrozoan *Apatizanclea* (right) (RC).

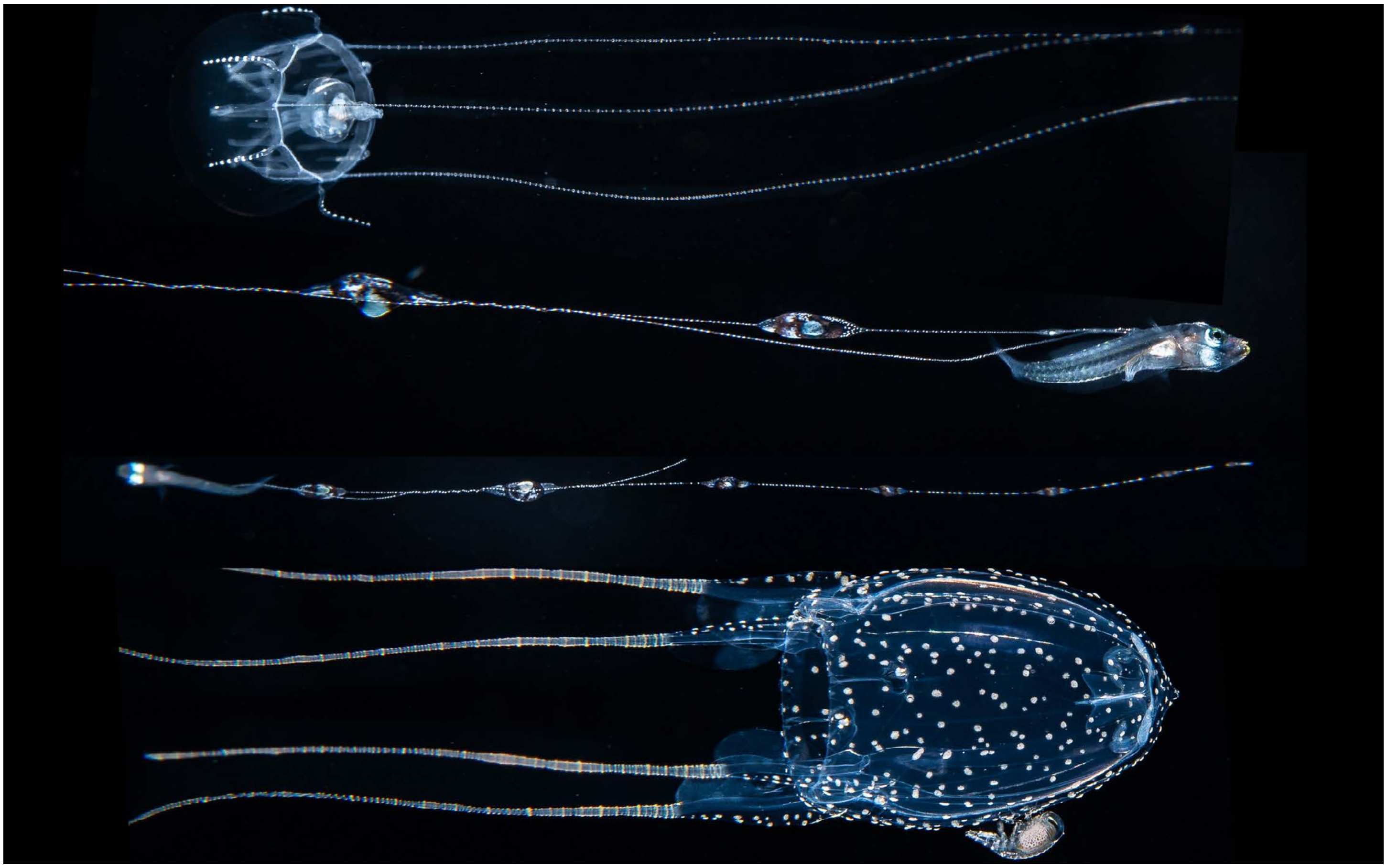


Figure 22. Putative mimicry by *Liopropoma* with elongate dorsal-fin spine filaments (center, lateral above, SM, ventral below, RC) to nematocyst-bearing tentacles of *Geryonia proboscidalis* (top) (RC) and cubozoan *Alatina alata* (bottom) (RC).

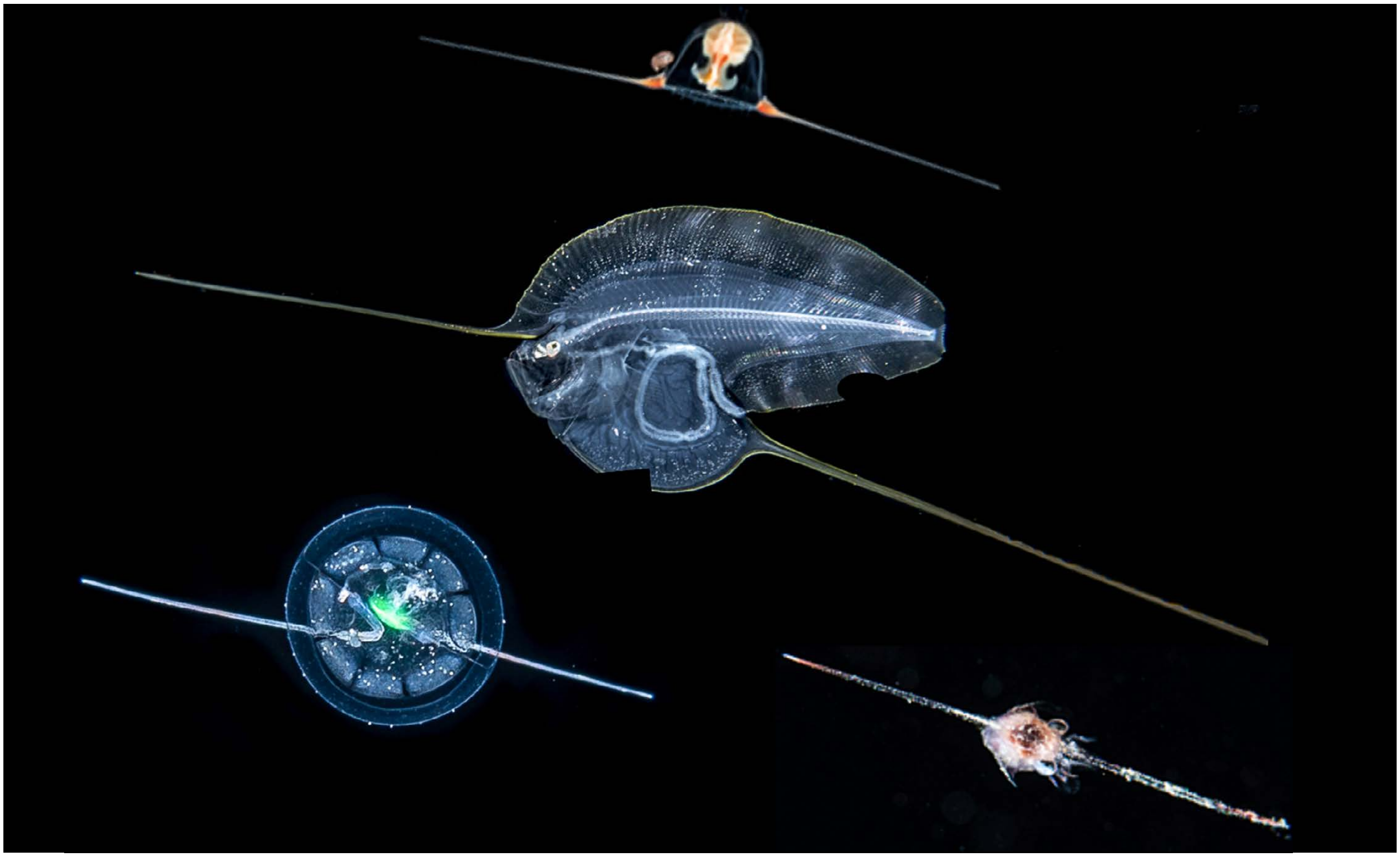


Figure 23. Putative mimicry by *Luciobrotula* showing the anterior dorsal-fin ray and posterior flexible filament (center) (FM) to hydromedusae such as *Amphinema rugosum* (top) (LI); the narcomedusa *Solmundella bitentaculata* (lower left) (RC) and a porcellanid crab zoea (lower right) (RC).

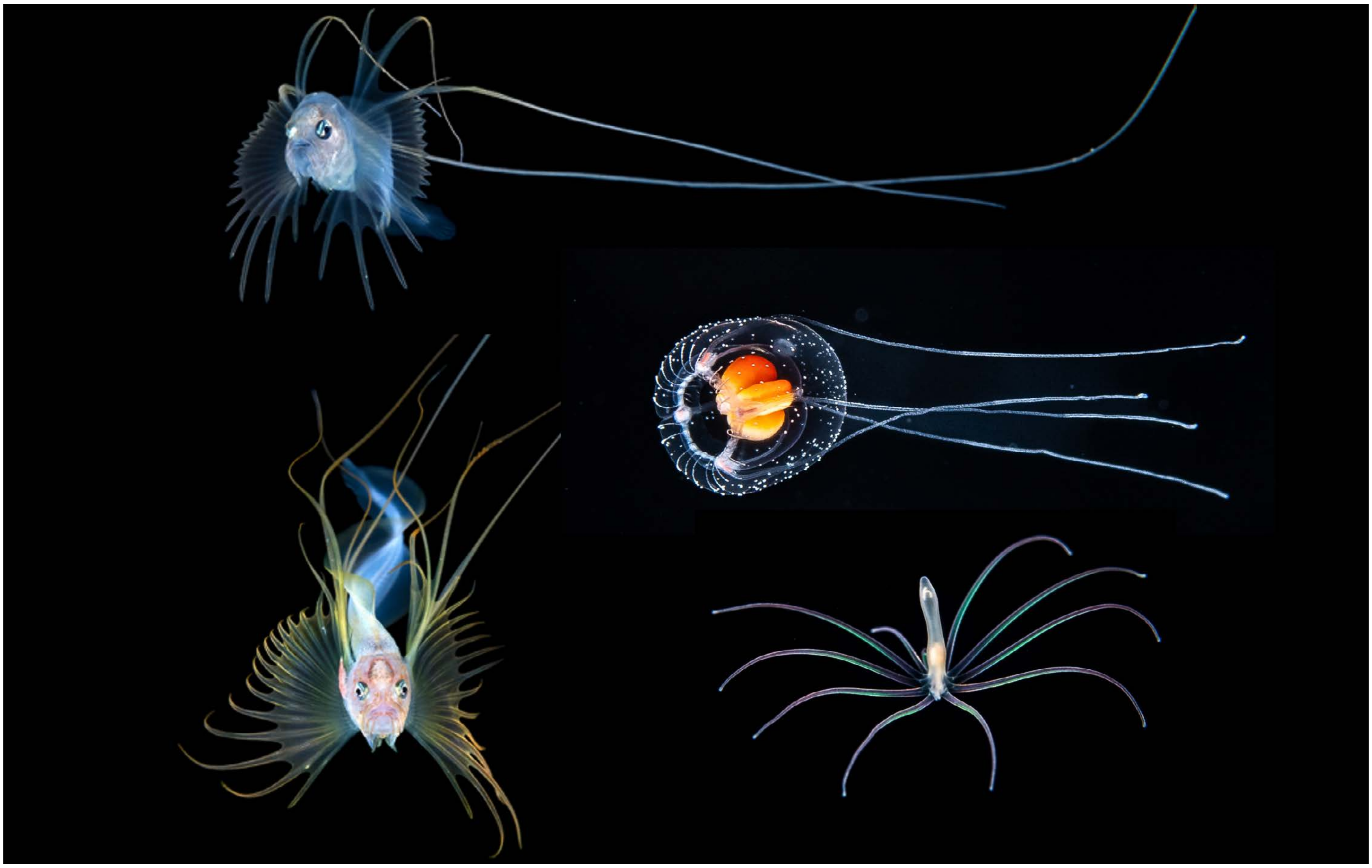


Figure 24. Putative mimicry by *Acanthonus myersi* showing the resemblance of elongate fin rays (pair at left) (SK) to the tentacles of a hydrozoan *Thecocodium quadratum* (center right) (RC) and a planktonic larval tube-anemone (Ceriantharia) (lower right) (RC).

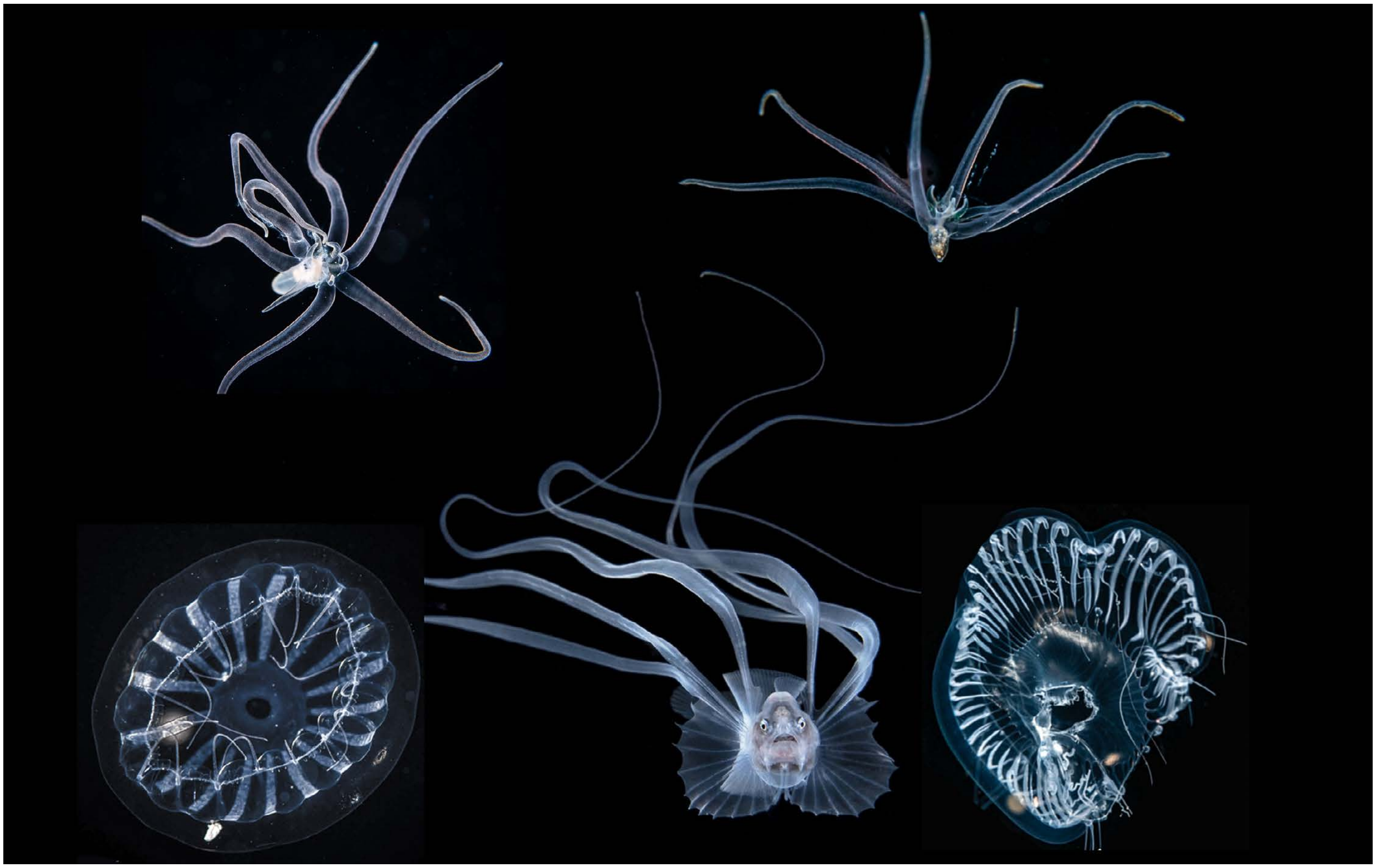


Figure 25. Putative mimicry by *Acanthonus armatus* (center) (DW) showing a strong resemblance to a larval tube-anemone (Ceriantharia) (top row) (RC) and hydromedusae *Cunina* (lower left) (RC) and *Aequorea* (lower right) (RC).

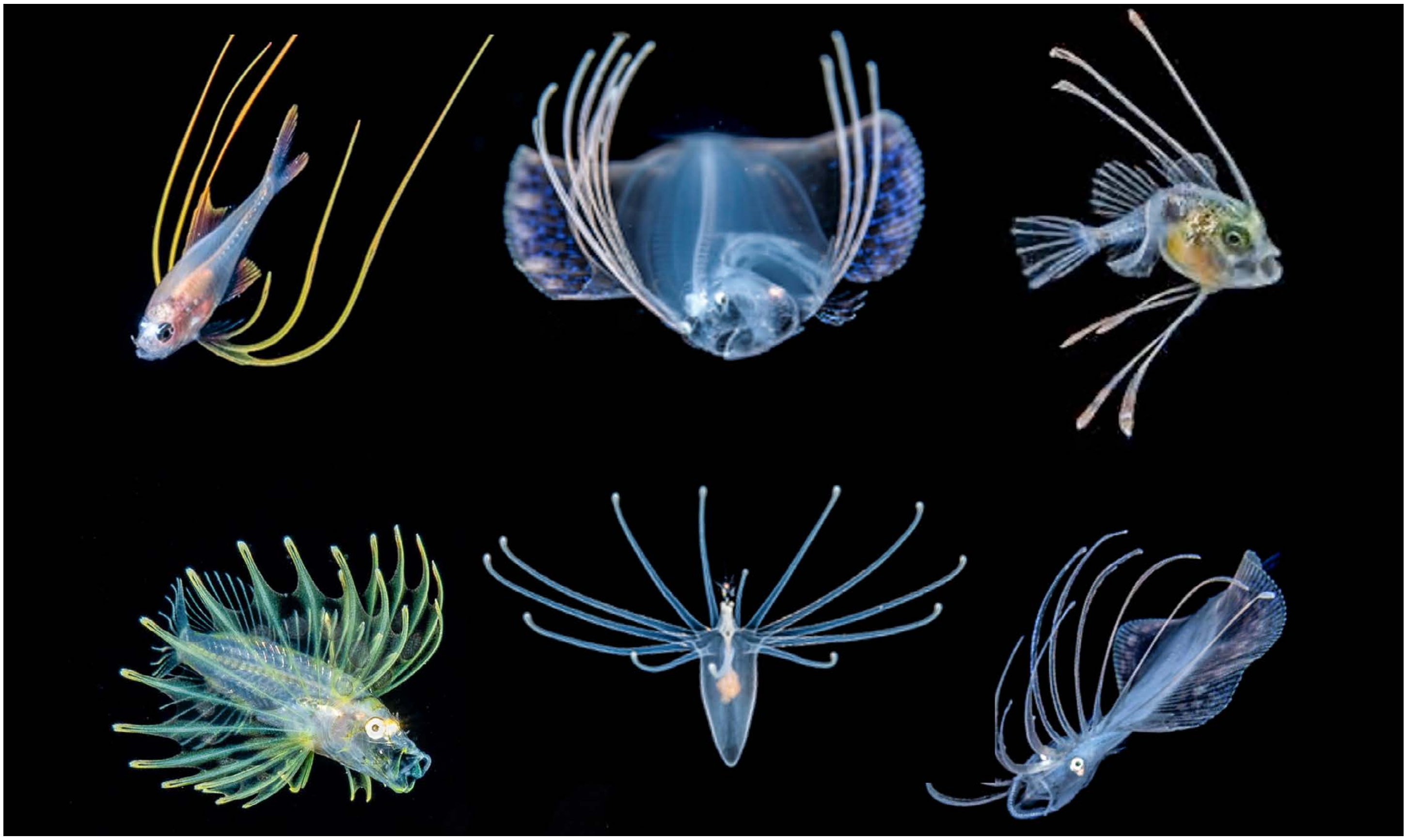


Figure 26. Putative mimicry by larval fishes showing the resemblance of elongate fin rays to tentacles of tube-anemone larvae (Ceriantharia) (lower center) (LI); (fishes clockwise from bottom left) *Pterois* (LI), *Beryx* (LI), *Cyclopsetta fimbriata* (MO), *Lophius* (ND), and *Cyclopsetta chittendeni* (MW).

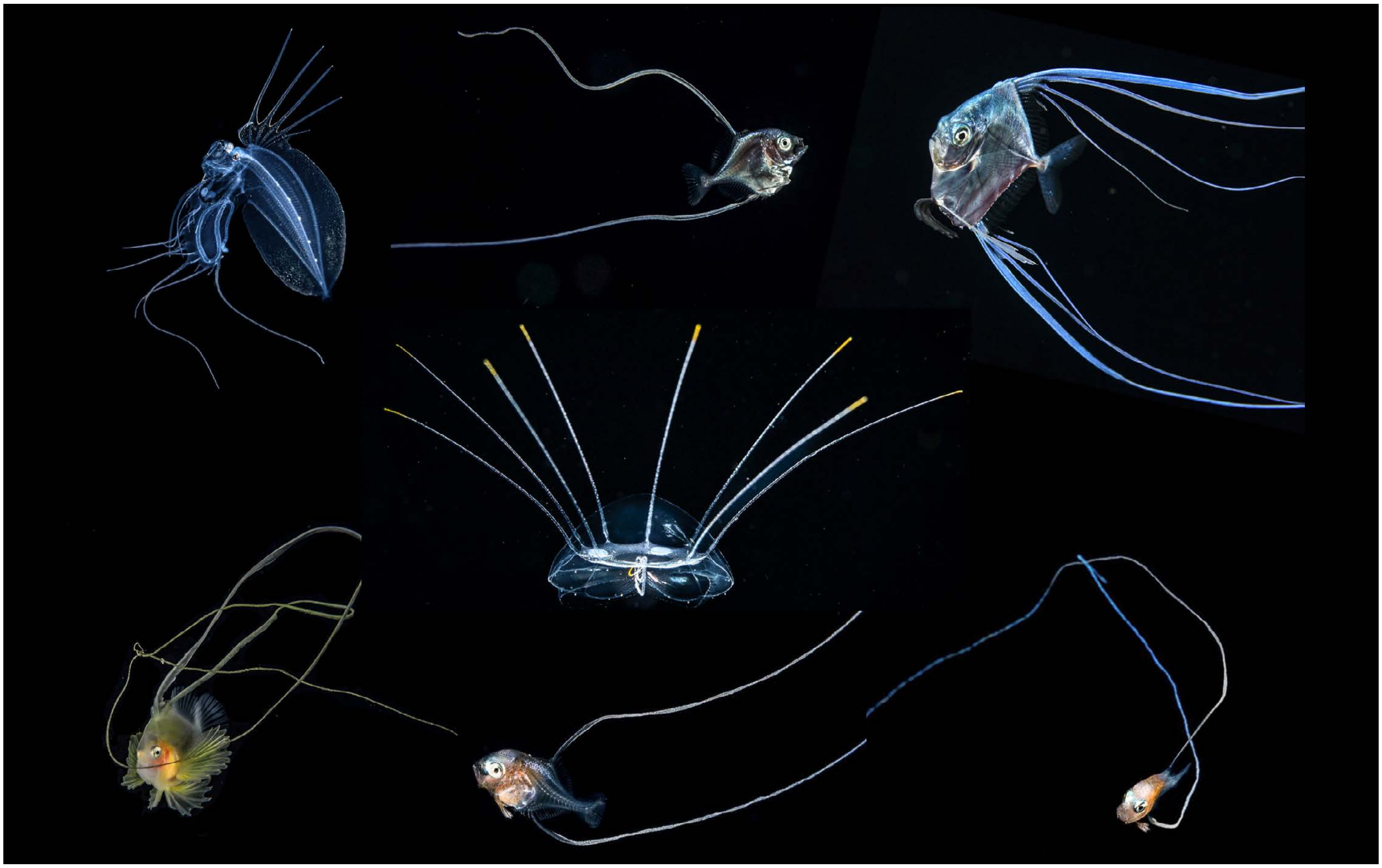


Figure 27. Putative mimicry by larval fishes showing the resemblance of elongate fin rays to tentacles of many cnidarians and ctenophores, e.g. hydrozoan *Solmaris flavofinis* (center) (RC); (fishes clockwise from bottom left) *Diploprion* (ST), unknown cusk eel (GH), and *Alectis ciliaris* (MO, MO, LI, LI).

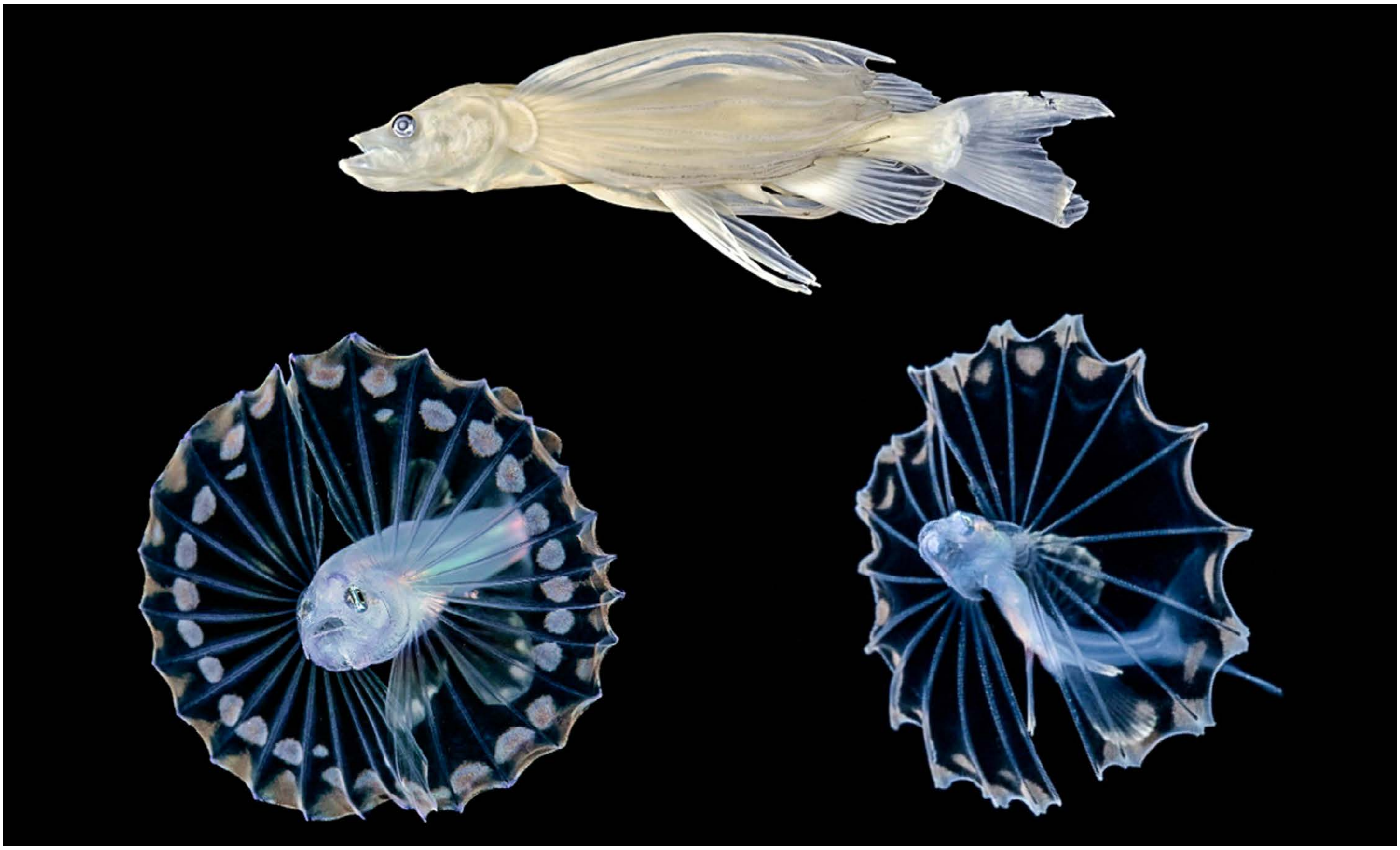


Figure 28. Putative mimicry by *Bathypterois* of common hydrozoans; not apparent in formalin-fixed specimen (top) (DJ)) showing the retracted position of pectoral fins typical of fixed specimens vs. flared circular display of pectoral fins in situ (left SK, right LI).

Figure 29. Putative mimicry by *Bathypterois* (upper row) (SK) showing remarkable similarity to hydrozoans *Octophialucium* (lower left) (RC) and *Aequorea* (center and lower right) (RC).

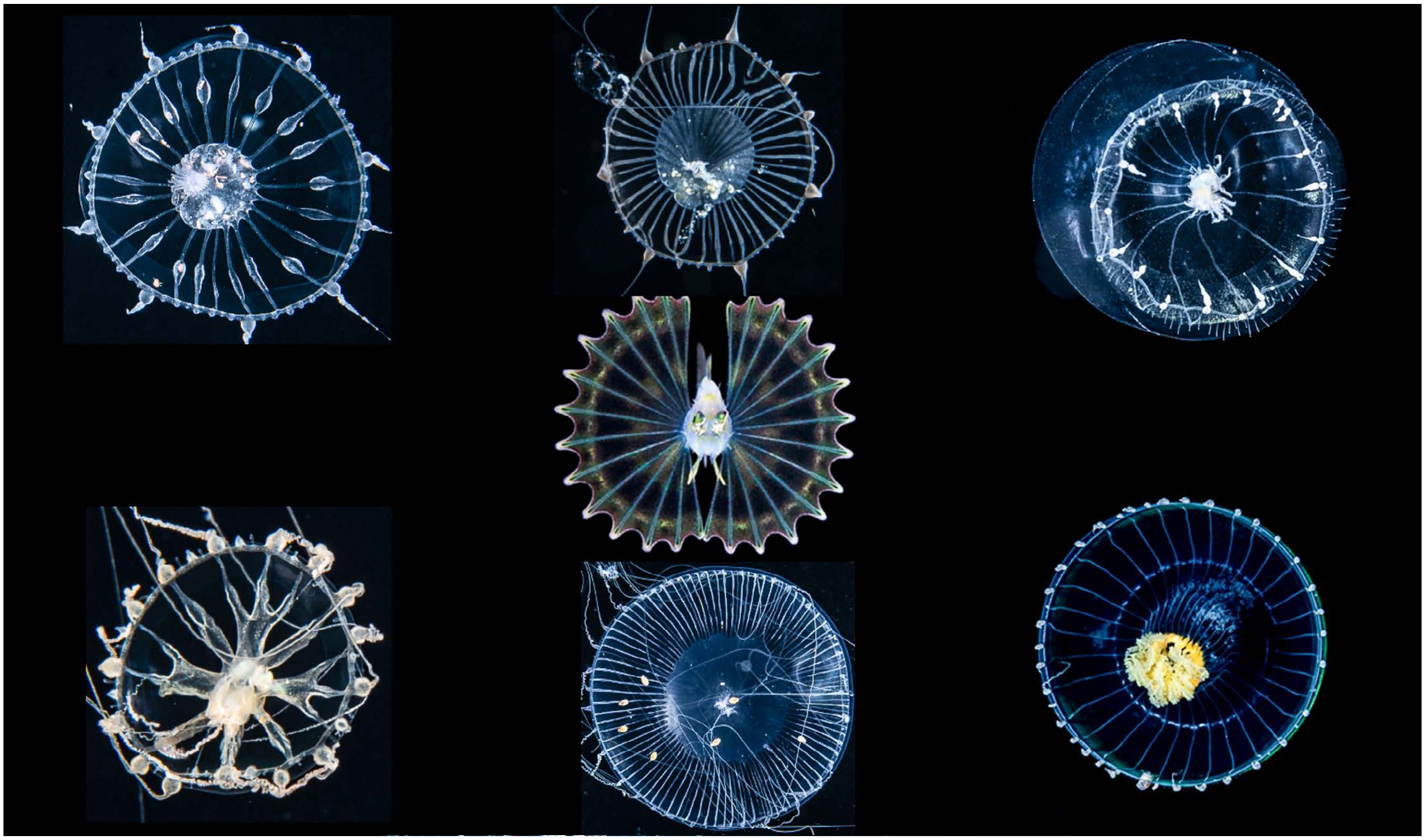


Figure 30. Putative mimicry by *Pterois* (center) (SK), showing remarkable similarity to hydrozoans (clockwise from lower left) *Staurodiscus*, *Aequorea*, *Aequorea*, *Orchistoma*, *Orchistoma*, and *Aequorea* (all RC).

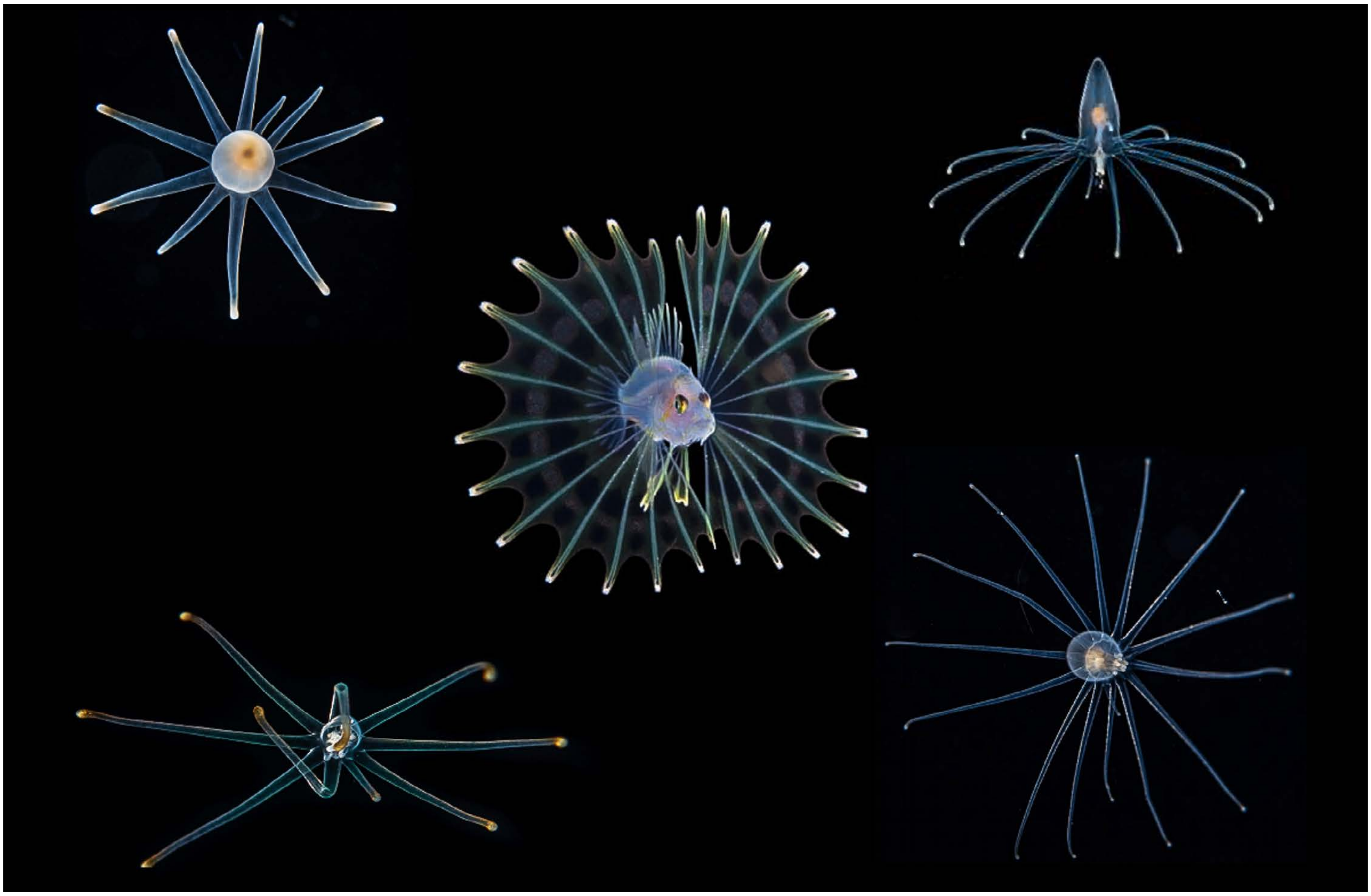


Figure 31. Putative mimicry by *Pterois* (center) (SK) showing similarity in the full fan-like fin-ray extension to various species of larval tube-anemones (Ceriantharia) (clockwise from bottom left: RC,RC,LI, RC).

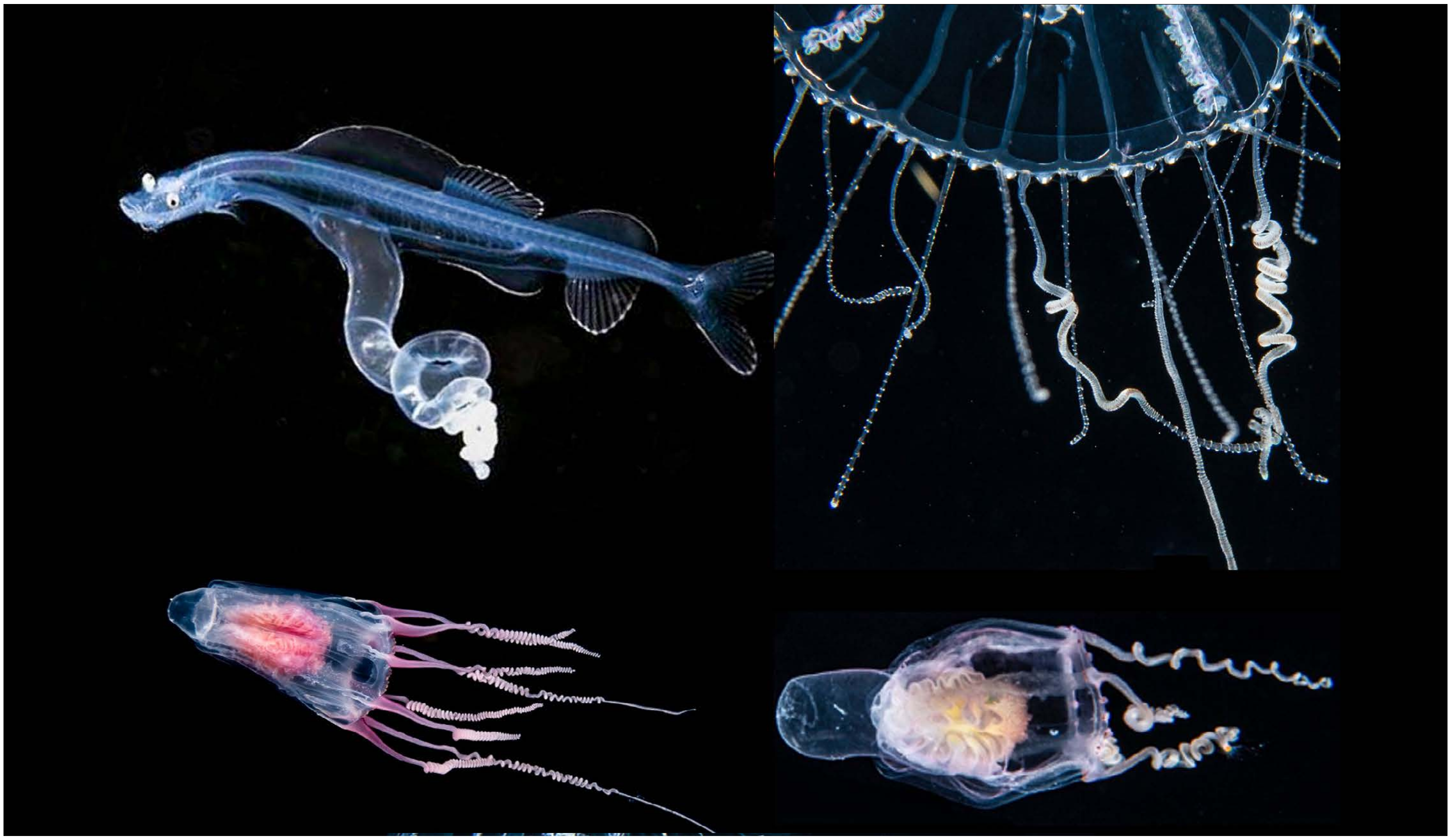


Figure 32. Putative mimicry by *Astronesthes* (upper left) (DW); its coiled gut shows a conspicuous similarity to the coiled tentacles of hydrozoans *Olindias tenuis* (top right) (RC), *Cirrhitiara superba* (lower right) (RC), and *Eutiara mayeri* (lower left) (LI).

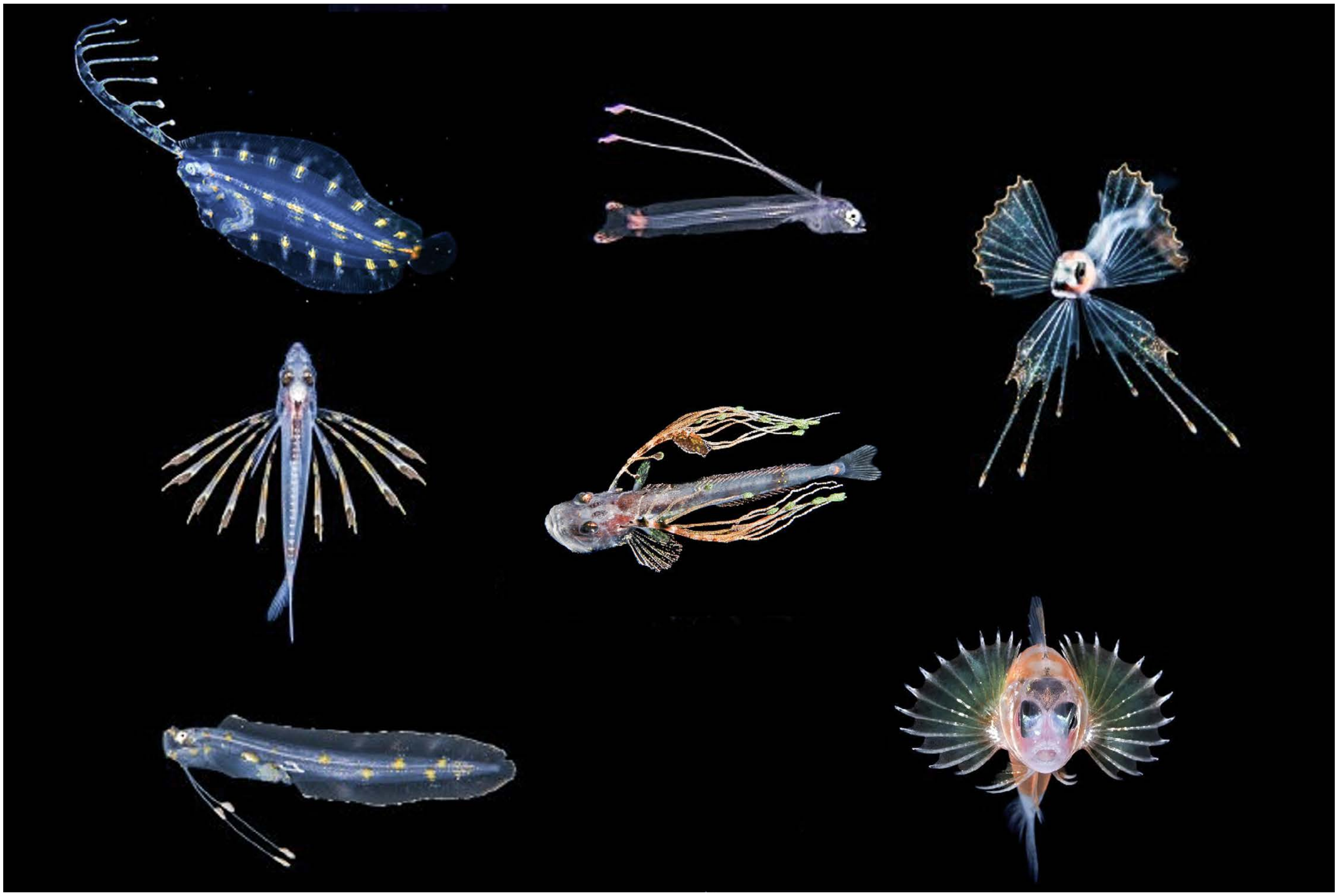


Figure 33. Larval fishes with exceptional embellishments that may also provide protection via Batesian mimicry: *Champsodon* (center) (ND) showing unusual elaborations of the opercular filament; (clockwise from upper left) *Arnoglossus* (RM), *Ipnops* (AB), *Chiasmodon* (AB), Blenniidae (AB), *Barathrites* (AB), and *Gymnapogon* (AB).

Protective commensalism

Protective commensalism is used here to describe an association between organisms where it is presumably advantageous to only one partner. In the examples recorded below, fishes or other invertebrates take advantage of noxious gelatinous zooplankton, not by mimicry but by intentional proximity to them. It is also possible that the gelatinous zooplankton also gain some unknown advantage. It is also possible that the gelatinous zooplankton suffer some bodily damage from the association or, in the case of phyllosomata, the gelatinous zooplankton are perhaps consumed during the association [28]. For example, among larval invertebrates, phyllosoma larva commonly carry one or more cnidarians or similar looking gelatinous zooplankton for protection from predators (Fig. 34). Some young fishes use a similar strategy by riding or biting onto noxious gelatinous zooplankton (Figs. 35 & 36). This behavior illustrates the value of seeking proximity to undesirable gelatinous zooplankton. It is also indirect evidence of the potential effectiveness for larval fishes to evolve physical traits that facilitate mimicry of gelatinous zooplankton.

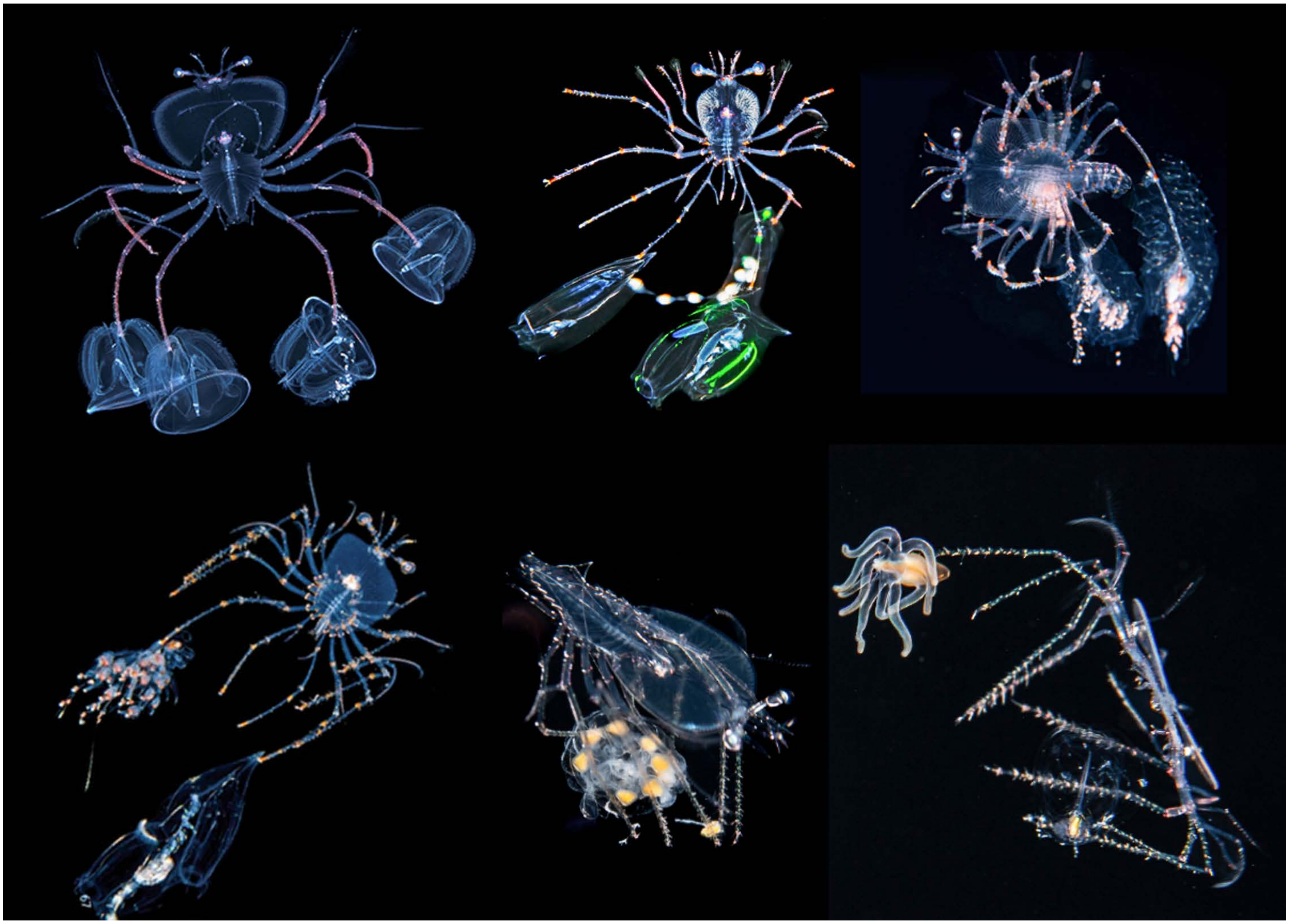
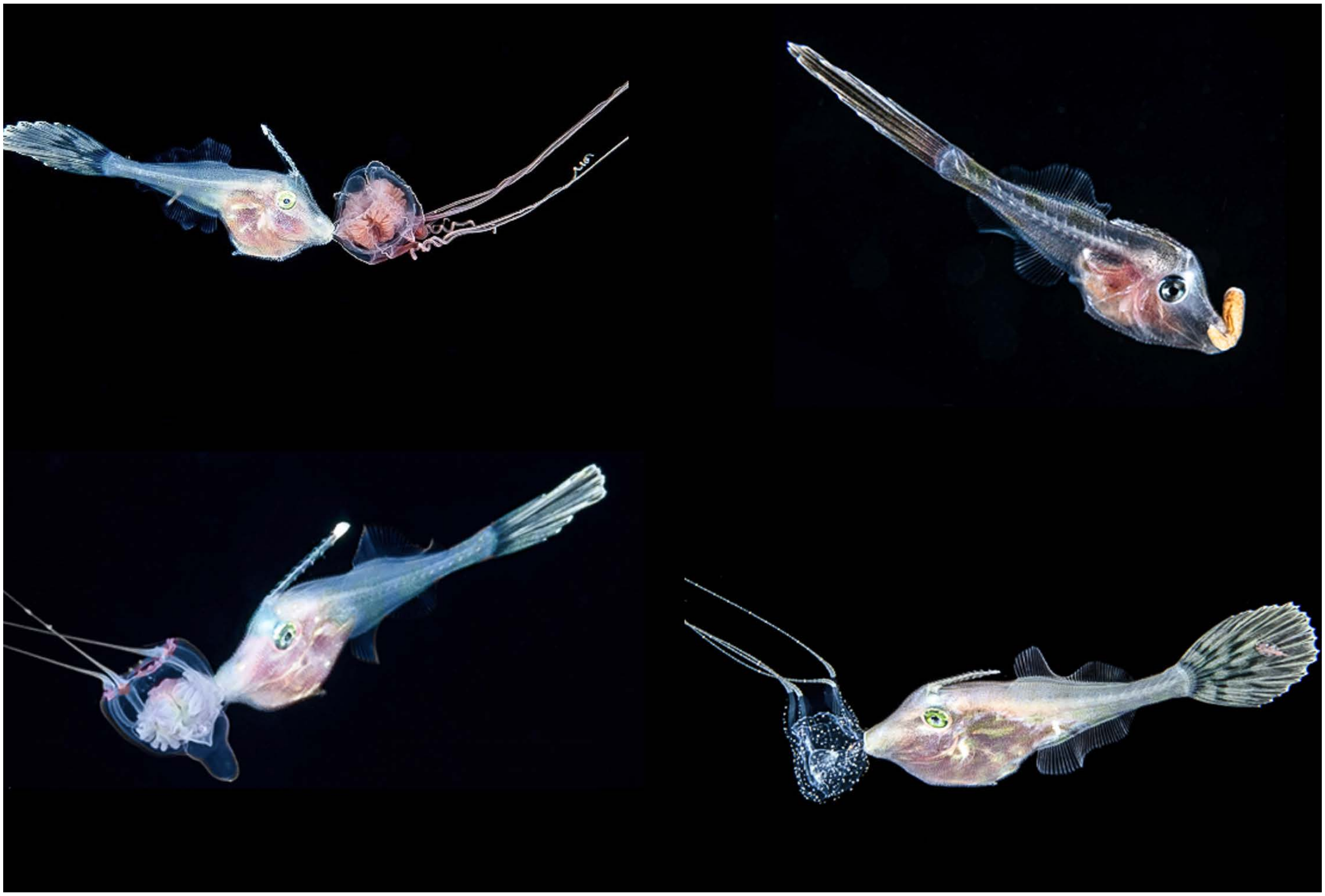
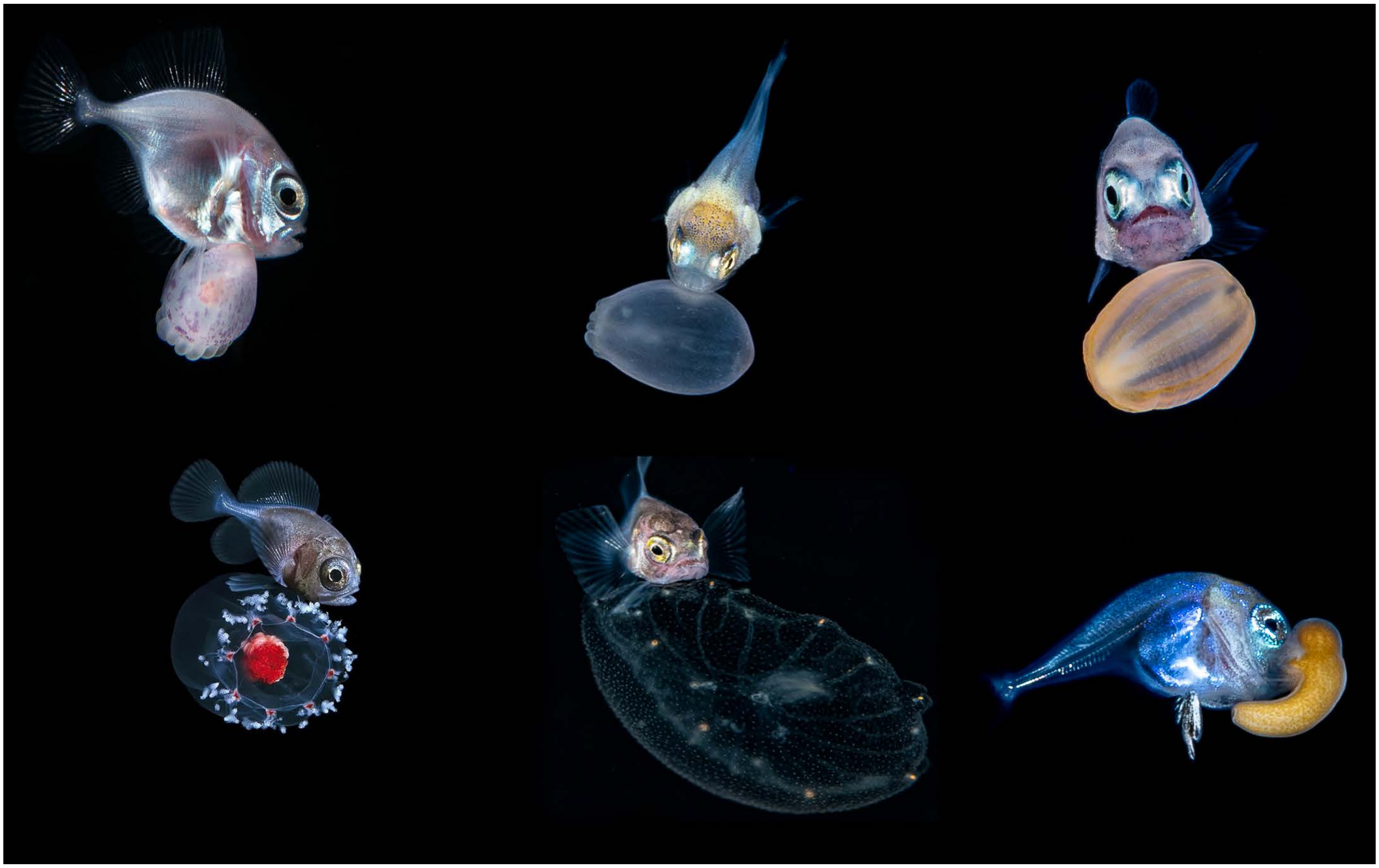


Figure 34. Protective commensalism: phyllosoma larvae holding various noxious gelatinous zooplankton: (clockwise from lower left) phyllosoma larva holding siphonophores (LI), tornaria larvae of *Enteropneusta* (SK), calycophorid siphonophores (ND), physonectid siphonophores (RC), a larval tube-anemone (Ceriantharia) (RC), and *Nausithoe* (Scyphozoa) (RC).

Figure 35 (next page, upper). Protective commensalism: *Aluterus* biting noxious gelatinous zooplankton (clockwise from bottom left) *Cirrhitiara superba* (LI), *Eutiara mayeri* (LI), *Zoantharia* larva (Semper's larva) (RC), and cubozoan *Alatina alata* (KZ).

Figure 36 (next page, lower). Protective commensalism: *Brama* with noxious gelatinous zooplankton (clockwise from bottom left) *Koellikerina fasciculata* (SK), larval anemones (Ceriantharia) (FM, LI, FM), *Zoantharia* larva (Semper's larva) (LI), and the hydrozoan *Aequorea* (RC).





Conclusions

Our knowledge of the form and coloration of many pelagic fish larvae has been limited by the condition of net-collected specimens, lack of direct observations of live fishes, and our ability to identify the species represented. The same limitations exist for the pelagic invertebrates, particularly “jellyfish”. Blackwater images have greatly facilitated visual comparisons. Several lines of circumstantial evidence strongly suggest that one of the ways that some pelagic fish larvae (particularly among neoteleosts) avoid predation is by Batesian mimicry of noxious, unpalatable, and/or low-caloric-value invertebrates, primarily cnidarians and ctenophores. The evidence includes both strong and more general resemblance of a wide taxonomic/phylogenetic variety (at least 15 orders and 30 plus families) of highly vulnerable fish larvae to specific gelatinous invertebrates, and the common physical association of some larval fishes with a variety of them. Additional research, particularly field observations and experimentation, is required to obtain direct evidence for the mimicry hypothesis. In addition we need a greater understanding of the anatomical constraints, swimming tradeoffs, and selective pressures associated with the evolution of the proposed Batesian mimicry. Data are required on comparative mortality rates and life-history characteristics such as the duration of larval life. Quantitative information on mimic and model distribution and abundance (on multiple time scales) is also lacking. Although this study has produced a strongly supported answer to the original question of why many larval oceanic fishes have extreme anatomical elaborations, many more challenging unknowns have arisen for future investigation.

List of Orders and Families

These taxa of marine fishes have larvae that display developmental features characteristic of, or that can be imputed to, Batesian mimicry. This list supports the assertion that there is widespread adaptive convergence of the proposed Batesian mimicry strategy. The goal of this list is to illustrate the remarkable taxonomic/phylogenetic diversity of the group and it is not meant to be an exhaustive or complete list [29,30].

Anguilliformes
multiple families
Stomiiformes
Stomiidae Bleeker, 1859
Aulopiformes
Ipnopidae Gill, 1884
Ateleopodiformes
Ateleopodidae Bonaparte, 1850
Myctophiformes
Myctophidae Gill, 1893
Lampridiformes
Trachipteridae Swainson, 1839
Gadiformes
Bregmacerotidae Gill, 1872
Moridae Moreau, 1881
Stephanoberyciformes
Barbourisiidae Parr, 1945
Cetomimidae Goode & Bean, 1895
Gibberichthyidae Parr, 1933
Melamphaidae Gill, 1893
Stephanoberycidae Gill, 1884
Beryciformes
Berycidae Lowe, 1839
Perciformes
Apogonidae Günther, 1859
Carangidae Rafinesque, 1815
Champsodontidae Jordan & Snyder, 1902
Chiasmodontidae Jordan & Gilbert, 1883
Epinephelidae Ogilby, 1899
Scorpaeniformes
Scorpaenidae Risso, 1827
Triglidae Rafinesque, 1815
Pleuronectiformes
Bothidae Smitt, 1892
Cyclopsettidae Campbell, Chanet, Jhen-Nien, Mao-Ying & Wei-Jen, 2019
Cynoglossidae Jordan, 1888
Paralichthyidae Regan, 1910
Blenniiformes
Blenniidae Rafinesque, 1810
Ophidiiformes
Carapidae Poey, 1867
Ophidiidae Rafinesque, 1810
Lophiiformes
Caulophrynidae Goode & Bean, 1896
Gigantactinidae Lophiidae Rafinesque, 1810
Ogcocephalidae Gill, 1893

Acknowledgements

Our good friend and colleague G. David Johnson passed away before we made a final submission of this paper. Dave had enormous enthusiasm for this project and we are very sorry that he did not live to see its publication. Photographs and specimens collected by blackwater divers kindled his imagination and offered clues to the mysteries of the weird and wonderful larval development of some marine fishes. Dave was a highly accomplished scholar, a generous collaborator and good friend. We will miss him.

Geoff Moser offered valuable advice and insight in numerous emails and phone calls with GDJ. His untimely demise left a significant void in our knowledge of the lives of larvae of marine fishes. We wish we could have continued to mine his insights and wise musings as we prepared this manuscript and that he could have reviewed it for us. We would also like to thank the following individuals for reading and commenting on early drafts of the manuscript: Gustav Paulay, Mike Fahay, Ron Thresher, and Nalani Schnell.

This paper would not have been possible without the enthusiastic efforts of so many amateur and professional divers and photographers listed below, who have refined blackwater diving and photography techniques and shared their expertise and their large collections of photographic material. We are very grateful for their support and for that of our charter boat operators, Pura Vida Divers and Walker's Dive Charters for providing the hundreds of charters used to explore the nighttime zooplankton off the Florida coast. We are particularly grateful for the large number of photographs contributed by Linda Ianniello and Steven Kovacs. We would also like to thank Ai Nonaka for technical assistance and the collection staff of the NMNH and FLMNH for specimen handling. This study was funded in part by the Herbert R. and Evelyn Axelrod Endowment for Systematic Ichthyology at NMNH to GDJ.

Photographer credits

The photographers, listed in the text by their initials, are Mike Bartick (MB), Anthony Berberian (AB), Richard Collins (RC), Dennis Corpuz (DC), Matthew D'Avella (MD), Ned Deloach (ND), Deb Devers (DD), Galice Hoaru (GH), Linda Ianniello (LI), Dave Johnson (DJ), Steven Kovacs (SK), Susan Mears (SM), Fabien Michenet (FM), Kevin Mattson (KM), Ryo Minemizu (RM), Michael Patrick O'Neill (MO), Walt Stearns (WS), Shawn Turek (ST), Michael Walker (MW), Andrea Whitaker (AW), Dennis Whitestone (DW), Eric Yee (EY), and Kat Zhou (KZ).

Literature Cited

1. Milisen, J.W., Matye, S.A. & Kobayashi, D.R. (2018) Nocturnal visual census of pelagic fauna using scuba near Kona, Hawai'i. *Pacific Science*, 72 (4), 399–410.
2. Greer, A., Woodson, C., Guigand, C. & Cowen, R. (2016) Larval fishes utilize Batesian mimicry as a survival strategy in the plankton. *Marine Ecology Progress Series*, 551, 1–12.
3. Nonaka, A., Milisen, J.W., Mundy, B.C. & Johnson, G.D. (2021) Blackwater Diving: an exciting window into the planktonic arena and its potential to enhance the quality of larval fish collections. *Ichthyology & Herpetology*, 109 (1), 138–156.
4. Schuchert, P. & Collins, R. (2021) Hydromedusae observed during night dives in the Gulf Stream. *Revue Suisse de Zoologie*, 128 (2), 237–356.
5. Schuchert, P. & Collins, R. (2024) Additional observations on hydromedusae during night dives in the Gulf Stream. *Revue Suisse de Zoologie*, 131 (1), 43–120.
6. Houde, E.D. (2002) Chapter 3. Mortality. *In*: Fuiman, L.A. & Werner, R.G. (Eds.), *Fishery science: The unique contribution of early life stages*. Blackwell Scientific Publishing, Oxford, UK, pp. 64–87.
7. Bates HW. (1862) Contributions to an insect fauna of the Amazon Valley. Lepidoptera, Heliconidae. *Transactions of the Linnean Society of London*, 23, 495–566.
8. Moser, H.G. (1981) Morphological and functional aspects of marine fish larvae. *In*: Lasker, R. (Ed.), *Marine fish larvae: Morphology, ecology, and relation to fisheries*, University of Washington Press, Seattle, WA, USA, pp. 89–131.
9. Johnson, G.D. (1984) Percoidei, Development and relationships. *In*: Moser. H.G. et al. (Eds.), *Ontogeny and Systematics of Fishes*, American Society of Ichthyologists and Herpetologists, Special Publication 1, pp. 464–498.

10. Khong, N.M.H., Yusoff, F.M., Jamilah, B., Basri, M., Maznah, I., Chan, K.W, et al. (2016) Nutritional composition and total collagen content of three commercially important edible jellyfish. *Food Chemistry*, 196, 953–960.
11. Amaoka, K. (1972) Studies on the larvae and juveniles of the sinistral flounders III, *Laeops kitaharae*. *Japanese Journal of Ichthyology*, 19, 154–165.
12. Fraser, T. & Smith, M. (1974) An exterilium larval fish from South Africa with comments on its classification. *Copeia*, 1974, p. 886.
13. Govoni, J., Olney, J., Markle, D. & Curtsinger, W. (1984) Observations on structure and evaluation of possible functions of the vexillum in larval Carapidae (Ophidiiformes). *Bulletin of Marine Science*, 34, 60–70.
14. De Sylva, D.P. & Eschmeyer, W.N. (1977) Systematics and biology of the deep-sea fish family Gibberichthyidae, a senior synonym of the family Kasidoroidae. *Proceedings of the California Academy of Sciences, 4th Series*, 41, 215–231.
15. Miller, M.J. (2023) 43 Years after H.G. Moser's Seminal "Morphological and Functional Aspects of Marine Fish Larvae": The Commonalities of Leptocephali and Larvae of Other Marine Teleosts. *Fishes*, 2023 (8), p. 548. https://doi.org/10.3390/fishes8110548
16. Kyle, H.M. (1913) Flat-fishes (Heterosomata). *Report on the Danish Oceanographical Expeditions 1908-10 to the Mediterranean and Adjacent Seas. Vol. 2 (Biology), A. Dana Report* (1), 1–150.
17. Hubbs, C.L. & Chu Y.T. (1934) Asiatic fishes (*Diploprion* and *Laeops*) having a greatly elongated dorsal ray in very large postlarvae. *Occasional Papers of the Museum of Zoology, University of Michigan*, 299, 1–17. https://deepblue.lib.umich.edu/handle/2027.42/56738
18. Yevseyenko, S.A. (1976) Larvae of *Bothus ocellatus* (Agassiz) from the northwest Atlantic. *Journal of Ichthyology*, 16 (4), 568–605.
19. Dawson, C.E., Yasuda, F. & Imai, C. (1979) Elongate dermal appendages in species of *Yozia* (Syngnathidae) with remarks on *Trachyrhamphus*. *Japanese Journal of Ichthyology*, 25 (4), 244–250.
20. Cushing, D.H. (1996) Towards a science of recruitment in fish populations. *In*: Kinne, O. (Ed.), *Excellence in Ecology, Book 7*. International Ecology Institute, Oldendorf/Luhe, Germany, 175 pp.
21. Kristiansen, T., Drinkwater, K.F., Lough, R.G. & Sundby, S. (2011) Recruitment Variability in North Atlantic Cod and Match-Mismatch Dynamics. *PLoS ONE*, 6 (3), e17456. https://doi.org/10.1371/journal.pone.0017456
22. Luo, J., Grassian, B., Tang, D., Irisson, J.O., Greer, A., Guigand, C. et al. (2014) Environmental drivers of the fine-scale distribution of a gelatinous zooplankton community across a mesoscale front. *Marine Ecology Progress Series*, 510, 129–149.
23. Cowen, R.K. & Guigand, C.M. (2008) In situ ichthyoplankton imaging system (ISIIS), system design and preliminary results. *Limnology and Oceanography: Methods*, 6 (2), 126–132.
24. Johnsen, S. (2014) Hide and seek in the open sea, pelagic camouflage and visual countermeasures. *Annual Review of Marine Science*, 6, 369–392.
25. Umeton, D., Read, J.C.A. & Rowe, C. (2017) Unravelling the illusion of flicker fusion. *Biology Letters*, 13 (2), 20160831. https://doi.org/10.1098/rsbl.2016.0831
26. Sundby, S. & Kristiansen, T. (2015) The Principles of Buoyancy in Marine Fish Eggs and Their Vertical Distributions across the World Oceans. *PLoS ONE*, 10 (10), e0138821. https://doi.org/10.1371/journal.pone.0138821
27. Sherratt, T.N. (2002) The evolution of imperfect mimicry. *Behavioral Ecology*, 13 (6), 821–826.
28. O'Rorke, R., Lavery, S.D., Wang, M., Gallego, R., Waite, A.M., Beckley, L.E. et al. (2015) Phyllosomata associated with large gelatinous zooplankton, hitching rides and stealing bites. *The ICES Journal of Marine Science* , 72 (1), i24–i27.
29. Wiley, E.O. & Johnson, G.D. (2010) A teleost classification based on monophyletic groups. *In*: Nelson, J.S., Schultze, H., Wilson, M.V.H., *Origin and Phylogenetic Interrelationships of Teleosts.* Verlag Dr. Friedrich Pfeil, Munich, Germany, pp. 123–182.
30. Fricke, R., Eschmeyer, W.N. & Van der Laan, R. (Eds.) (2024) *Eschmeyer's Catalog of Fishes: Genera, Species, and References*. San Francisco (California Academy of Sciences). Electronic version accessed 10 February 2025 at http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp