

## Colour morph of a probable queen angelfish *Holacanthus ciliaris* from Dry Tortugas, Florida

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An unusual colour morph of a probable *Holacanthus ciliaris* was observed in Dry Tortugas, Florida, which can possibly be explained by recessive homozygosity, however, further testing is necessary. This variation of *H. ciliaris* has previously only been described at St Paul's Rocks, Mid-Atlantic Ridge.

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Many reef fish species are brightly coloured and show remarkable pigment variation, yet little is known about the evolutionary significance of colour patterns (McMillan *et al.*, 1999; Rocha *et al.*, 2007). Variation in colour patterns among fishes are actually attributed to a variety of causes including the following: hybridization (Feddern, 1968; Pyle & Randall, 1994), inbreeding (Edwards & Lubbock, 1983), genetic differentiation (Planes & Doherty, 1997), environmental influence (Medioni *et al.*, 2001), reproductive behaviour and mood (Thresher & Moyer, 1983), sexual dichromatism (Gilmore & Jones, 1992; Tuz-Sulub *et al.*, 2006), mimicry (Munday *et al.*, 2003), melanism (Colin, 1982), disease (Rahn *et al.*, 2004), encysted parasites (Roberts, 1975) and injury (Dawson, 1967). Colour polymorphism is distinguished from other colour variations by a fixed change that may be genetically determined and may persist and drive speciation (Domeier, 1994; Puebla *et al.*, 2007; Rocha *et al.*, 2007). Colour morphs may result from the effects of founding events by a small number of individuals, reinforced by geographic isolation and genetic differentiation (Edwards & Lubbock, 1983; Luiz Jr., 2003a) or hybridization between species. Multiple colour morphs may be sympatric or interbreed, possibly influenced by sexual and natural selection, producing intermediate coloured hybrids (Planes & Doherty, 1997). Examples of polymorphism are found within the families Serranidae (Domeier, 1994; Medioni *et al.*, 2001), Cirrhitidae (DeMartini & Donaldson, 1996), Syngnathidae (Guimarães, 1999), Ostraciidae (Pattengill-Semmens, 1999) and Pomacentridae (Planes & Doherty, 1997; Feitoza *et al.*, 2003), among others.

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Numerous colour morphs in the queen angelfish *Holacanthus ciliaris* (L.) have previously only been observed at St Paul's Rocks, a small group of isolated rocky islands along the Mid-Atlantic Ridge, 1000 km east of the Brazilian equatorial coast (Lubbock & Edwards, 1981; Feitoza *et al.*, 2003; Luiz Jr., 2003a, b). The distinctive colours of St Paul's populations of *H. ciliaris* were considered unique to that area until a similarly coloured *H. ciliaris* was observed during visual assessments of reef fisheries resources within the marine protected area ('Research Natural Area') of the Dry Tortugas National Park, Florida (DRTO; 24°40'27" N; 82°54'12" W) on 22 June 2006. This is the first sighting of an *H. ciliaris* colour morph outside the population of St Paul's Rocks.

*Holacanthus ciliaris* are closely related to blue angelfish *Holacanthus bermudensis* Goode, and colouration is the only reliable character to separate these species (Feddern, 1968) [Fig. 1(a), (b)]. Throughout their tropical western Atlantic distribution, from Brazil to Bermuda, adult *H. ciliaris* are typically bright blue and yellow. Individuals are distinguished from *H. bermudensis* by a dark blue-ringed ocellated forehead, a blue and black area at the base of the pectoral fin, a bright yellow caudal fin and an orange tint across the preopercula and the caudal, pelvic and pectoral fins (Allen *et al.*, 1998; Debelius *et al.*, 2003). Yellow and green colour phases are occasionally observed and fish from insular populations (Caribbean, Bahamas and Bermuda) are generally more brightly coloured than those from continental coastal environments (Allen *et al.*, 1998).

The high occurrence of unusual colour morphs in *H. ciliaris* at St Paul's Rocks (c. 5%; Lubbock & Edwards, 1981) is attributed to inbreeding in a small isolated population (Edwards & Lubbock, 1983; Joyeux *et al.*, 2001; Luiz Jr., 2003a). Three predominant colour morphs were described: (1) yellow or orange, (2) blue and (3) white. Numerous variations of these three main types, however, have also been reported (Lubbock & Edwards, 1981; Feitoza *et al.*, 2003; Luiz Jr., 2003b). St Paul's Rocks is isolated from Brazilian and West African coastal reefs and may sustain itself by self-recruitment due to its remote location and the dynamics of the westward South Equatorial Current and eastward Equatorial Countercurrent (Jones *et al.*, 1999; Swearer *et al.*, 1999; Robertson, 2001; Feitoza *et al.*, 2003; Rocha, 2003). The relatively shallow (40–150 m) Atlantic Equatorial Undercurrent, which occasionally reaches the surface and flows east past St Paul's Rock when the South-East Trade Winds fail, may be primarily influential in bringing larval reef fish recruits from the Brazilian western Atlantic Ocean (Stalcup & Parker, 1965; Bowen, 1966; Lubbock & Edwards, 1981; Edwards & Lubbock, 1983; Feitoza *et al.*, 2003).

The Tortugas specimen, 200 mm total length ( $L_T$ ), observed at 1610 hours on a small patch reef (8.84 m depth), was predominately a cobalt blue morph, with blue pigment extending into the dorsal fin with white pectoral, pelvic and caudal fins, the latter with a dark blue border along the posterior edge [Fig. 1(c)]. The colouration on the exposed posterior edge of the large scales on the body appeared white. The snout and opercula areas were asymmetrically mottled white with cobalt blue. The dorsal and anal fins both contained areas of deep yellow-orange as well as areas of albinism, with soft ray filaments that attenuated well beyond the caudal fin. This fish also had the following features: an ocellus on the forehead, with the ring and interior disc somewhat indefinite; a darkened blue pectoral fin base with small black markings and a wide blue stripe at the dorsal posterior edge

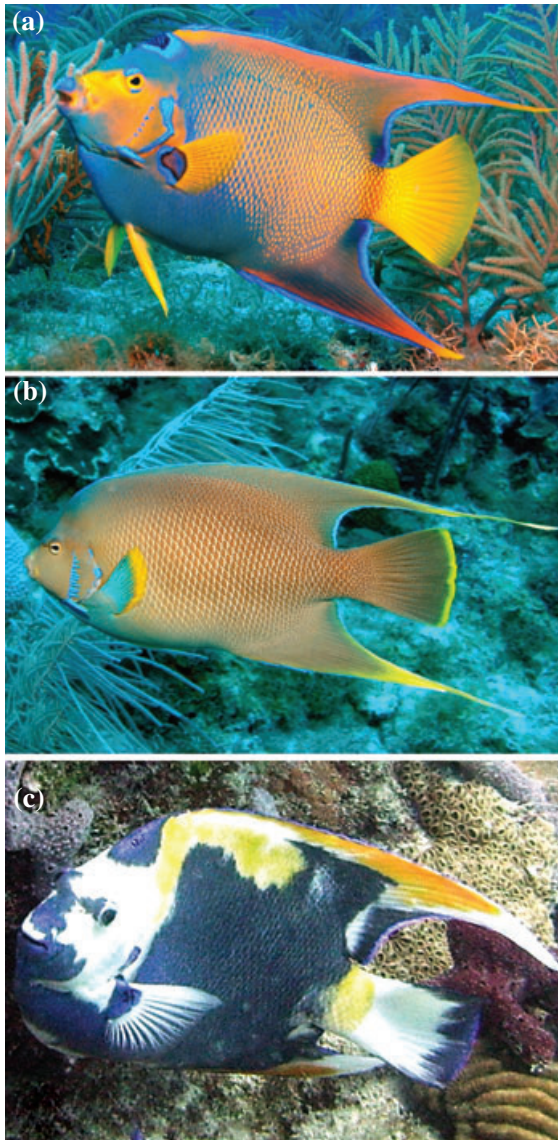


FIG. 1. Typical pigmentation exhibited by (a) *Holacanthus ciliaris*, (b) *Holacanthus bermudensis* and (c) probable *H. ciliaris* colour morph from Dry Tortugas National Park, Florida.

of the operculum. These traits tend to be attributed to *H. ciliaris* or intermediate hybridization patterns between *H. ciliaris* and *H. bermudensis* (Feddern, 1968). There was no gross evidence of disease or externally expressed lesions associated with the hypopigmented tissue.

The hybridization hypothesis could explain the presence of the unusual colour morphology described here, since *H. ciliaris*, *H. bermudensis* and the rock beauty *Holacanthus tricolor* (Bloch) all inhabit the Dry Tortugas region. Fecund fishes from all three species are known to occur simultaneously at least in the late

spring in the Caribbean (Munro *et al.*, 1973). Interspecific hybridizations among fishes are known to occur naturally and particularly among marine angelfishes (Pomacanthidae; Pyle & Randall, 1994). In the western Atlantic Ocean, angelfish hybridizations have been identified between grey angelfish *Pomacanthus arcuatus* (L.) x French angelfish *Pomacanthus paru* (Bloch) and *H. bermudensis* x *H. ciliaris* (Feddern, 1968; Pyle & Randall 1994). The latter is sometimes mistakenly identified as the Townsend angelfish, *Angelichthys townsendi*, which was first described by Nichols & Mowbray (1914) based on a hybrid between *H. ciliaris* and *Holacanthus isabelita* (Jordan & Rutter) (Feddern, 1968) (note that *H. isabelita* is a junior synonym of *H. bermudensis*). Even though it is not recognized as a valid species, this hybrid is fairly common in the Florida Keys, Bahamas and Gulf of Mexico (Robins *et al.*, 1986). *Holacanthus ciliaris* x *H. bermudensis* registered hybrids possess colouration intermediate between these species (Feddern, 1968; Allen, 1978; Robins *et al.*, 1986) and appear distinctively dissimilar from the Tortugas specimen.

The Tortugas angelfish closely resembles a white and brown type documented by the Cambridge Expedition to St Paul's Rock in 1979 (Lubbock, 1980). This fish is unlikely as a recruit from the *H. ciliaris* population at St Paul's, however, considering the great geographic distance between the two areas. Larval exchange between the Brazilian western Atlantic Ocean and the insular Caribbean through surface currents is thought to be restricted by a biogeographical barrier (Amazon River freshwater outflow), although there is evidence it may occur on a limited basis (Rocha, 2003). Furthermore, all colour morphs of *H. ciliaris* from St Paul's Rocks are characterized by relatively short dorsal and anal fin filaments (Feitoza *et al.*, 2003; Luiz Jr., 2003*b*). In the general *H. ciliaris* population these filaments are long by comparison and trail beyond the posterior edge of the caudal fin (Feitoza *et al.*, 2003). Therefore, the Tortugas angelfish described here is probably not a diseased fish, nor a *Holacanthus* hybrid, nor a recruit from St Paul's Rocks. Overall similarities in colour and morphology suggest it is probably a rare, recessive, homozygous expression of a Tortugas population of *H. ciliaris*. This hypothesis can only be elucidated by comparative phylogeographic and morphological studies that clarify the role of hybridization, gene flow and selection for colour patterns within *H. ciliaris*.

The Tortugas are located south of the western Florida Shelf and at the western terminus of the Florida Keys archipelago. Since larval transport in the area is predominately driven by the Florida Current westward, the Dry Tortugas may be considered intermediately isolated. Paris *et al.* (2005) state regional connectivity *via* the Loop Current across deep waters with Cuba and the Yucatan is significantly limited. Fixed changes in colour patterns tend to occur faster in isolated populations like those at St Paul's Rocks as a result of natural selection and genetic drift (Palumbi, 1994; Luiz Jr., 2003*a*; Chakraborty *et al.*, 2006). Consequently, phenotypic expression of recessive traits due to higher frequencies of homozygous genes occurs (Futuyma, 1998). This may explain why colour morphs are rare throughout the range of *H. ciliaris* but relatively common at St Paul's Rocks.

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### References

- Allen, G. R. (1978). *Butterfly and Angelfishes of the World*, Vol. 2. New York, NY: John Wiley & Sons.
- Allen, G. R., Steene, R. & Allen, M. (1998). *A Guide to Angelfishes and Butterflyfishes*. Perth, Australia: Odyssey Publishing, Tropical Reef Research.
- Bowen, V. T. (1966). St. Paul's on the subway. *Oceanus* **12**, 2–4.
- Chakraborty, A., Venugopal, M. N., Hidaka, K. & Iwatsuki, Y. (2006). Genetic differentiation between two colour morphs of *Gerres erythrourus* (Perciformes: Gerreidae) from the Indo-Pacific region. *Ichthyological Research* **53**, 185–188.
- Colin, P. L. (1982). Melanism in the rock beauty, *Holacanthus tricolor*, (Pisces: Pomacanthidae) in Puerto Rico. *Bulletin of Marine Science* **32**, 800–802.
- Dawson, C. E. (1967). Three new records of partial albinism in American Heterosomata. *Transactions of the American Fisheries Society* **96**, 400–404. doi: 10.1577/1548-8659(1967)96[400:TNROPA]2.0.CO;2
- Debelius, H., Tanaka, H. & Kuitert, R. H. (2003). *Angelfishes: a Comprehensive Guide to Pomacanthidae*. Chorleywood, UK: TMC Publishing.
- DeMartini, E. E. & Donaldson, T. J. (1996). Color morph-habitat relations in the arc-eye hawkfish *Paracirrhites arcatus* (Pisces: Cirrhitidae). *Copeia* **1996**, 362–371.
- Domeier, M. L. (1994). Speciation in the serranid fish *Hypoplectrus*. *Bulletin of Marine Science* **54**, 103–141.
- Edwards, A. & Lubbock, R. (1983). Marine zoogeography of St Paul's Rocks. *Journal of Biogeography* **10**, 65–72.
- Feddern, H. A. (1968). Hybridization between the western Atlantic angelfishes *Holacanthus isabelita* and *H. ciliaris*. *Bulletin of Marine Science* **18**, 351–382.
- Feitoza, B. M., Rocha, L. A., Luiz Jr., O. J., Floeter, S. R. & Gasparini, J. L. (2003). Reef fishes of St. Paul's Rocks: new records and notes on biology and zoogeography. *Aqua, Journal of Ichthyology and Aquatic Biology* **7**, 61–82.
- Futuyma, D. J. (1998). *Evolutionary Biology*. Sunderland, MA: Sinauer Associates, Inc.
- Gilmore, R. G. & Jones, R. S. (1992). Color variation and associated behaviour in the epinepheline groupers, *Mycteroperca microlepis* (Goode and Bean) and *M. phenax* Jordan and Swain. *Bulletin of Marine Science* **51**, 83–103.
- Guimarães, R. Z. P. (1999). Chromatic and morphologic variation in *Halicampus crinitus* (Jenyns) (Teleostei: Syngnathidae) from southeastern Brazil, with comments on its synonymy. *Revue Française d'Aquariologie et Herpetologie* **26**, 7–10.
- Jones, G. P., Milicich, M. J., Emslie, M. J. & Lunow, C. (1999). Self-recruitment in a coral reef fish population. *Nature* **402**, 802–804.
- Joyeux, J.-C., Floeter, S. R., Ferreira, C. E. L. & Gasparini, J. L. (2001). Biogeography of tropical reef fishes: the South Atlantic puzzle. *Journal of Biogeography* **28**, 831–841. doi: 10.1046/j.1365-2699.2001.00602.x
- Lubbock, R. (1980). Die Insel der "Hai-Society". Auf der Suche nach neuen Riffbarschen an den St. Paul's Felsen. *Aquarien Magazin* **11**, 626–630.

- Lubbock, R. & Edwards, A. (1981). The fishes of Saint Paul's Rocks. *Journal of Fish Biology* **18**, 135–157. doi: 10.1111/j.1095–8649.1981.tb02810.x
- Luiz Jr., O. J. (2003a). Colour morphs in a queen angelfish *Holocanthus ciliaris* (Perciformes: Pomacanthidae) population of St. Paul's Rocks, NE Brazil. *Tropical Fish Hobbyist* **51**, 82–90.
- Luiz Jr., O. J. (2003b). The quest for *ciliaris* morphs. In *Angelfishes: a Comprehensive Guide to Pomacanthidae* (Debelius, H., Tanaka, H. & Kuitert, R. H., eds), pp. 70–73. Chorleywood, UK: TMC Publishing.
- McMillan, W. O., Weigt, L. A. & Palumbi, S. R. (1999). Color pattern evolution, assortative mating, and genetic differentiation in brightly colored butterflyfishes (Chaetodontidae). *Evolution* **53**, 247–260.
- Medioni, E., Lecomte Finiger, R., Louveiro, N. & Planes, S. (2001). Genetic and demographic variation among colour morphs of cabrilla sea bass. *Journal of Fish Biology* **58**, 1113–1124. doi: 10.1006/jfbi.2000.1522
- Munday, P. L., Eyre, P. J. & Jones, G. P. (2003). Ecological mechanisms for coexistence of colour polymorphism in a coral-reef fish: an experimental evaluation. *Oecologia* **442**, 519–526. doi: 10.1007/s00442-003-1356-7
- Munro, J. L., Gaut, V. C., Thompson, R. & Reeson, P. H. (1973). The spawning seasons of Caribbean reef fishes. *Journal of Fish Biology* **5**, 69–84. doi: 10.1111/j.1095–8649.1973.tb04431.x
- Nichols, J. T. & Mowbray, L. L. (1914). A new angel-fish (*Angelichthys townsendi*) from Key West. *Bulletin of the American Museum of Natural History* **33**, 581–583.
- Palumbi, S. R. (1994). Genetic divergence, reproductive isolation, and marine speciation. *Annual Review of Ecology and Systematics* **25**, 547–572.
- Paris, C. B., Cowen, R. K., Claro, R. & Lindeman, K. C. (2005). Larval transport pathways from Cuban snapper (Lutjanidae) spawning aggregations based on biophysical modeling. *Marine Ecology Progress Series* **296**, 93–106.
- Pattengill-Semmens, C. V. (1999). Occurrence of a unique color morph in the smooth trunkfish (*Lactophrys triqueter* L.) at the Flower Garden Banks and Stetson Bank, northwest Gulf of Mexico. *Bulletin of Marine Science* **65**, 587–591.
- Planes, S. & Doherty, P. J. (1997). Genetic relationships of the colour morphs of *Acanthochromis polyacanthus* (Pomacentridae) on the northern Great Barrier Reef. *Marine Biology* **130**, 109–117.
- Puebla, O., Bermingham, E., Guichard, F. & Whiteman, E. (2007). Colour pattern as a single trait driving speciation in *Hypoplectrus* coral reef fishes? *Proceedings of the Royal Society B* **274**, 1265–1271. doi: 10.1098/rspb.2006.0435
- Pyle, R. L. & Randall, J. E. (1994). A review of hybridization in marine angelfishes (Perciformes: Pomacanthidae). *Environmental Biology of Fishes* **41**, 127–145.
- Rahn, J. J., Gibbs, P. D. L. & Schmale, M. C. (2004). Patterns of transcription of a virus-like agent in tumor and non-tumor tissues in bicolor damselfish. *Comparative Biochemistry and Physiology C* **138**, 401–409. doi: 10.1016/j.cca.2004.06.008
- Roberts, R. J. (1975). The effects of temperature on diseases and their histopathological manifestations in fish. In *The Pathology of Fishes* (Ribelin, W. E. & Migaki, G., eds), pp. 477–496. Madison, WI: University of Wisconsin Press.
- Robertson, D. R. (2001). Population maintenance among tropical reef fishes: inferences from small-island endemics. *Proceedings of the National Academy of Sciences of the United States of America* **98**, 5667–5670.
- Robins, C. R., Ray, C. G., Douglass, J. & Freund, R. (1986). *A Field Guide to Atlantic Coast Fishes of North America*. New York, NY: Houghton Mifflin Company.
- Rocha, L. A. (2003). Patterns of distribution and processes of speciation in Brazilian reef fishes. *Journal of Biogeography* **30**, 1161–1171. doi: 10.1046/j.1365–2699.2003.00900.x
- Rocha, L. A., Craig, M. T. & Bowen, B. W. (2007). Phylogeography and the conservation of coral reef fishes. *Coral Reefs* **26**, 501–512. doi: 10.1007/s00338-007-0261-7
- Stalcup, M. C. & Parker, C. E. (1965). Drogue measurements of shallow currents on the equator in the Western Atlantic Ocean. *Deep-Sea Research* **12**, 535–536.

- Swearer, S. E., Caselle, J. E., Lea, D. W. & Warner, R. R. (1999). Larval retention and recruitment in an island population of coral-reef fish. *Nature* **402**, 799–802.
- Thresher, R. E. & Moyer, J. T. (1983). Male success, courtship complexity and patterns of sexual selection in three congeneric species of sexually monochromatic and dichromatic damselfishes (Pisces: Pomacentridae). *Animal Behavior* **31**, 113–127.
- Tuz-Sulub, A., Brulé, T., Cervera-Cervera, K. & Espinoza-Mendez, J. C. (2006). Evidence for sexual dichromatisms in spawning aggregations of yellowfin grouper *Mycteroperca venenosa* and tiger grouper *Mycteroperca tigris* from the southern Gulf of Mexico. *Journal of Fish Biology* **69**, 1744–1755. doi: 10.1111/j.1059–8649.2006.01241