INVITED PERSPECTIVES AND REVIEWS

Learning and Behavior in Reef Fish: Fuel for Microevolutionary Change?

Joshua A. Drew* & Jennifer M. Gumm†

* Department of Ecology, Evolution and Environmental Biology, Columbia University, New York, NY, USA
† Department of Biology, Stephen F. Austin State University, Nacogdoches, TX, USA

Abstract

Small-scale population differentiation among coral reef fishes may be more common than previously thought. New molecular technologies have informed patterns of differentiation, while experimental approaches focusing on larval abilities to limit distribution have explored processes leading to diversification. Building upon a recently published paper by Wismer et al. that examined population level differences in learning and cooperative behaviors in cleaner wrasse (*Labroides dimidiatus*), we use a phylogenetic framework to explore how social behaviors are distributed among wrasses in the Labrichthyines clade. Establishing links between social behavior and speciation across the phylogeny allows us explore how social behaviors such as learning and cooperation may also act as possible mechanisms driving diversification at the microevolutionary scale.

Introduction

In a recent piece, Wismer et al. (2014) demonstrated learned behavioral differences between two groups of a common reef fish *Labroides dimidiatus* (Labridae) living in different habitats, patch reefs, and continuous fringing reefs. In our piece, we aim to use the fascinating observational and experimental work performed by Wismer et al. as an entry point into how learned behaviors could potentially join biogeography and behavior as mechanisms explaining the observed diversity of reef fish population structure. Over the past 15 yr, a body of work has emerged suggesting that marine species which were previously considered geographically widespread are actually groups of closely related and range restricted species (Terry et al. 2000; Colborn et al. 2001; Taylor & Hellberg 2005; Drew et al. 2008, 2010; DiBattista et al. 2011, 2012; Drew & Kaufman 2012; Liu et al. 2012; Bernardi 2013). We now know that the evolutionary mosaic of marine species is much more finely partitioned and that factors such as local ecological conditions can play a major role in the evolutionary history of fishes (Rocha et al. 2005; Dawson 2012).

Labroides dimidiatus: phylogenetic perspective

The bluestriped cleaner wrasse, *L. dimidiatus* (Valenciennes, 1839: Labridae) is a common inshore fish, present from East Africa through the Central Pacific (Randall 2005). Juvenile *L. dimidiatus* settle out of the pelagos at approx. 20 d (Victor 1986). As juveniles, they have distinctly different coloration than adults and have the ability to facultatively switch between adult and juvenile colorations for some time before becoming fully mature (Mahon 1994). Adults live in male dominated harems that control access to a small home range, which includes one to several cleaning stations. Groups typically consist of one dominant male and up to six mature females (Robertson & Hoffman 1977).

There are five valid species in the genus *Labroides,* all of which are obligate cleaners (Fig. 1; Adam & Horii 2012). Within this genus, we see three patterns of sociality. The allopatrically distributed *L. dimidiatus* forms large groups of 5–12 individually cleaning adults and associated juveniles where they solicit clients through a stereotypical cleaning dance above cleaning stations which may exist for multiple
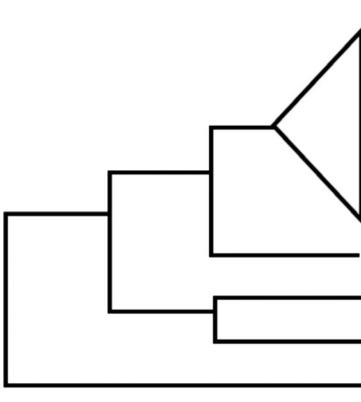
Species	Juvenile diet	Adult diet	Group size	Citation
Labroides dimidiatus	Obligate cleaner	Obligate cleaner	2-12 individuals	Randall (1958)
Labroides phthirophagus	Obligate cleaner	Obligate cleaner	2-5 individuals	Randall (1958)
Labroides pectoralis	Obligate cleaner	Obligate cleaner	Solitary or pairs	Randall (1958)
Labroides rubrolabiatus	Obligate cleaner	Obligate cleaner	Pairs of adults plus juveniles	Randall (1958)
Labroides bicolor	Obligate cleaner	Roving obligate cleaner	Single	Randall (1958)
Larabicus quadrilineatus	Obligate cleaner	Coral polyps	Unreported	Froukh & Kochzius (2007)
Diproctacanthus xanthurus	Obligate cleaner	Coral polyps	'Small groups'	Cole (2010)
Labropsis australis	Cleaner	Coral polyps	Unreported	Randall (1981)
Labrichthys unilineatus	Coral polyps	Coral polyps	Unreported	Cole (2010)

Fig. 1: Phylogenetic relationship among select Labrichthyines based on Cowman et al. (2009) and Westneat & Alfaro (2005).

generations (Grutter 2012). The sympatrically distributed Pacific species *L. pectoralis* and *L. rubrolabiatus* and the Hawaiian endemic *L. phthirophagus* also maintain cleaning territories but do so in smaller groups, typically in pairs. Lastly *L. bicolor* maintains the obligate cleaning trophic role of its congeners but instead of their sedentary and social lifestyle, they have a more active, solitary one. A roaming cleaner, *L. bicolor* has been seen swimming up to clients and actively soliciting them for cleaning (Randall 1958).

Thus, within this genus, we see two methods of stationary cleaning (large groups *L. dimidiatus,* small groups *L. pectoralis, L. phthirophagus,* and *L. rubrolabiatus*) and an example of transient client searching (*L. bicolor*). Within the fishes that maintain a defined cleaning station, we see the highly contrasting stripe, stereotypical of many cleaner fishes Arnal et al. (2006), typically terminating in a dark patch on the caudal fin. The mobile cleaner, *L. bicolor*, however, has a cleaner stripe on the anterior portion of its body, but that stripe terminates above the anal fin, and dissipates into a brightly colored posterior flank and caudal fin. These variations in coloration may help signal the various methods of feeding.

The genus *Labroides* lies within the Labrichthyines clade, which also includes the monotypic genera *Labrichthys, Diproctacanthus* and *Larabicus* and the polytypic *genus Labropsis* with six species (Fig 1). The non-*Labroides* members of Labrichthyines are exclusively coral mucus/polyp eaters as adults, with the basal member *Labrichthyes uniliniatus* being an obligate coral mucus and polyp eater as both a juvenile and an adult. The rest of the non-*Labroides* members of this group having obligate or facultative cleaning as juveniles. All members are either asocial or have very small group sizes. This phylogenetic relationship demonstrates a move from (coral) mucus eating to obligate cleaning, and a commensurate increase in group size, wherein nutritional benefit not only comes from the ectoparasites, but also from the scales and mucus of the clients (Grutter 1997; Grutter & Bshary 2004; Cole 2010). In this phylogenetic context, the links between species, and therefore speciation, are associated with changes in group size and feeding behavior.

Ecological effects on cheating

In the Wismer et al. (2014) study, we see that populations of *Labroides* on continuous reefs, where clients have options of many different cleaner stations, were less likely to cheat and adhered to the behavioral predictions made by game theory. By contrast, those found on patch reefs cheated more than expected. Juveniles had no initial differences in how they behaved but apparently adopted the cheating/non-cheating strategy of their host population. Wismer et al. highlight how the social environment may play a role in this pattern. Specifically, they propose that learning to cooperate may be limited on patch reefs due to a simple social environment in which less frequent interactions with clients decreases the benefit to learning and increases the time needed for learning.

The pattern of cheating on the patch reef may be influenced by the behavior and ecology of the clients as well. Wismer et al. point out that lower density of cleaners on patch reefs limits the ability of clients to exert choice of non-cheater cleaners. We propose that an additional reason why patch reef individuals are able to cheat more than predicted may be due to the geographic isolation of the relatively small patch reef compared to the continuous fringe reef. Most adult reef fish are site attached (Chapman & Kramer 2000)

and moving out of their preferred habitat presumably exposes them to higher rates of predation (Dahlgren & Eggleston 2000). Because of this spatial fidelity and increased chance of predation, we hypothesize that client species are making a calculated decision to remain at this site, despite low service quality providing cleaners, because the costs incurred by cheating cleaners are less than the cost of moving to another reef and the risk of increased predation during that move.

Resource availability has been shown to underlie geographic variation in cleaning behavior *L. dimidiatus*. Bansemer et al. (2002) examined *L. dimidiatus* from different reefs and found that the sites also differed in the local abundance of ectoparasites on clients. Sites that had clients with fewer ectoparasites also had cleaners that bit at client mucus more often. That is, lack of ectoparasites on clients led to more cheating by cleaners. The sites in this study were approx. 1000 km apart; however, ectoparasite emergence within a site may differ between substrate types (coral vs. sand; Jacoby & Greenwood 1988). Ectoparasite size also varies based on location within a reef (Jones & Grutter 2007), further suggesting that small-scale differences in ectoparasite loads may also contribute to variation in cleaning and cooperation between reef types.

Potential for speciation

Because many coral reef fish, including *L. dimidiatus* have pelagic durations lasting over several weeks (Victor 1986), traditionally they had been viewed as open populations. In this theoretical framework, there would be a strong selection for behavioral plasticity in larvae, because there is little chance the environment that the larvae would settle in would be similar to that of the parents. Therefore, traits that bestowed selective advantages to the parents may not offer the same benefit to the larvae (Warner 1997). However, in the past 15 yr, a suite of analytical methods have suggested that larval life histories do not necessarily result in populations that are as open as once thought. For example, modeling has suggested that oceanic currents can influence the distribution and the restriction of larvae (Treml et al. 2012), which has been seen in empirical studies (Galarza et al. 2009; Drew & Barber 2012). Additionally, larvae are not simply passive during this stage and a number of behaviors also contribute to the local retention of larvae, which is, a necessary but not sufficient precursor for small-scale speciation. We now know that larval fish have extensive sensory capabilities, including the use of

olfactory (Gerlach et al. 2007), auditory (Radford et al. 2011), visual (Igulu et al. 2011), and sun compass (Mouritsen et al. 2013) cues. Moreover in addition to being able to sense the reef, reef fish larvae as young as 7 d can respond to these cues with directional swimming (Fisher & Bellwood 2002). Thus, both ecological and behavioral traits help to set the stage for potential isolation of marine species on reef systems. For behaviorally mediated speciation to take place, the reproductive fitness of the adults that follow the locally 'appropriate' behaviors would need to exceed the proportion of larvae settling in inappropriate habitats. Selection may then favor offspring that retain behaviors that were advantageous to the parents as opposed to a generalist behavioral platform. There is much empirical work left to be performed to explore these possibilities, but they represent an exciting future direction in research.

The *Labroides* populations outlined in Wismer et al. (2014) represent a system where not adhering to the spatially explicit local market conditions incurs a loss of reproductive fitness. While the evolutionary history for *Labroides* populations on Lizard Island may be unclear, *Labroides* spp. evolved from cleaner/mucus eaters in the past, which indicates coupled change in morphology and behavior leading to speciation (Westneat et al. 2005). This could happen in two stages.

First, if differences in fish behavior based on different local conditions become translated into genotypic differences, then there is a mechanism for selection. For example, while the genetic and neurological underpinnings of cooperation remain yet unexplored in *Labroides*, and if there was selection for 'cooperativeness' in continuous reef populations and that genetic suite was carried over in offspring, then, those larvae settling in patch reefs would be put at a competitive disadvantage. Over time these differences in reproductive outputs could carry along other parts of the genome and ultimately could lead to fixed genetic differences.

Second, the difference in behavior must ultimately contribute to reproductive isolation. The structure of the breeding system with one larger male and multiple smaller females means that for those individuals who cheat on a continuous reef and cause a client to leave a station, breeding group members may have lower fitness (Raihani et al. 2010, 2012); thus, there is an evolutionary mechanism to enforce a group dynamic of cooperation and adherence to the predictions of game theory. By contrast, in theory, an individual who does not cheat on a patch reef will incur a relative loss of fitness, as they will be forgoing the

increased caloric value gained by cheating. The group dynamic provides an avenue for the evolution of sexual isolation as well. On continuous reefs, the large male will punish females who cheat by aggressively chasing them (Raihani et al. 2012). This is thought to have a twofold advantage for the male. First, punishment will reinforce the cooperation, which will benefit group as a whole by retaining clients. Second, females that cheat and eat high-quality mucus may be more likely to grow faster and reach a size at which they change sex and become a reproductive competitor. Thus, by punishing females, males are decreasing the likelihood of direct sexual competition with that individual. On patch reefs, it will be important to establish in future work if punishment is still a component of the breeding system. If it is not, there could be associated changes in life history traits related to changing sex, sexual selection related to density of male competitors, and ultimately could contribute to reproductive isolation between the populations on continuous and patch reefs.

Species with slightly different habitats can have differentiated genotypes, even if those habitats spatially close. Rocha et al. (2005) showed that inshore and off shore populations of the same species of wrasse were much more closely related to conspecifics living in the same habitat 1000s of kms away than to those living in a different habitats an order of magnitude closer. In this case, small-scale ecological differences were far better at predicting genetic differences then *a priori* predictions made by biogeography. There is evidence for genomic rearrangements in different ecotypes occur in Salmonids (Rogers & Bernatchez 2007; Rogers et al. 2013), Cichlids (Seehausen et al. 2008), and Sticklebacks (Malek et al. 2012) implying that ecological speciation over small spatial scales is an important feature in the evolution of a taxonomically diverse group of fishes. Additionally, there is variation in both the genetics and morphology within *L. dimidiatus* at Lizard Island, suggesting that the population is variable across both morphological and genetic diversity characters at a level not seen in other populations of *L. dimidiatus* (Sims et al. 2014), suggesting that the raw genetic diversity necessary for speciation may already exist on these reefs.

Summary

With the advent of high-resolution molecular markers, we have come to understand just how complex the distribution of biodiversity on reefs actually is, both within and among closely related species.

The existence of range restricted evolutionary distinct populations in organisms that have external fertilization and development has been one of the outstanding questions in marine biology over the past 25 yr. Initially, researchers focused on oceanography as one potential limit to dispersal (Barber et al. 2002). Subsequently, there was an acknowledgment that larvae had both the sensory modalities and developmental abilities necessary for self-agency (Gerlach et al. 2007).

Here, we integrate a phylogenetic perspective of social behavior and cooperation among a subgroup of Labridae species to inform an exploration of the potential of learned behavior as another mechanism that may contribute to small-scale population differentiation. We show how throughout their evolution there has been a connection between feeding behavior and group size at the macroevolutionary scale, and we ask the question whether similar behavioral differences may be driving differentiation at the microevolutionary scale?

Differences in behavior, which can lead to lowered fitness coupled with differences in the geographic distribution of where those behaviors are expressed, *could* provide an environment where those behavioral differences become fixed and ultimately result in speciation. The Wismer et al. (2014) paper does not fully address whether this scenario is happing in Lizard Island, and further research, including common tank experiments, would go far to fully exploring this tantalizing situation. However, we wish to take this opportunity to explore a thought experiment that highlights the importance of behavior, natural history observations, and learning can have in explaining the vivid spender of coral reef diversity.

Acknowledgements

Literature Cited

Adam, T. C. & Horii, S. S. 2012: Patterns of resource-use and competition for mutualistic partners between two species of obligate cleaner fish. Coral Reefs **31**, 1149—1154.

Arnal, C., Vernaeau, O. & Desdevises, Y. 2006: Phyloge-netic relationships and evolution of cleaning behaviour in the family Labridae: importance of body colour pattern. J. Evol. Biol. **19**, 755—763.

Bansemer, C., Grutter, A. S. & Poulin, R. 2002: Geographic variation in the behaviour of the cleaner wrasse *Labroides dimidiatus* (Labridae). Ethology **108**, 353—366.

Barber, P. H., Palumbi, S. R., Erdmann, M. V. & Moosa, M. K. 2002: Sharp genetic breaks among populations of *Haptosquilla pulchella* (Stomatopoda) indicate limits to larval transport: patterns, causes, and consequences. Mol. Ecol. **11**, 659—674.

Bernardi, G. 2013: Speciation in fishes. Mol. Ecol. **22**, 5487—5502.

Chapman, M. R. & Kramer, D. L. 2000: Movements of fishes within and among fringing coral reefs in Barbados. Environ. Biol. Fishes **57**, 11—24.

Colborn, J., Crabtree, R. E., Shaklee, J. B., Pfeiler, E. & Bowen, B. W. 2001: The evolutionary enigma of bonefishes (*Albula* spp.): cryptic species and ancient separations in a globally distributed shorefish. Evolution **55**, 807—820.

Cole, A. J. 2010: Cleaning to corallivory: ontogenetic shifts in feeding ecology of tubelip wrasse. Coral Reefs **29**, 125—129.

Cowman, P. F., Bellwood, D. R. & van Herwerden, L. 2009: Dating the evolutionary origins of wrasse lineages (Labridae) and the rise of trophic novelty on coral reefs. Mol. Phylogenet. Evol. **52**, 621—631.

Dahlgren, C. P. & Eggleston, D. B. 2000: Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. Ecology **81**, 2227.

Dawson, M. N. 2012: Parallel phylogeographic structure in ecologically similar sympatric sister taxa. Mol. Ecol. **21**, 987—1004.

DiBattista, J. D., Wilcox, C., Craig, M. T., Rocha, L. A. & Bowen, B. W. 2011: Phylogeography of the pacific blueline surgeonfish, *Acanthurus nigroris*, reveals high genetic connectivity and a cryptic endemic species in the Hawaiian archipelago. J. Mar. Biol. **2011**, 17.

DiBattista, J. D., Waldrop, E., Bowen, B. W., Schultz, J. K., Gaither, M. R., Pyle, R. L. & Rocha, L. A. 2012: Twisted sister species of pygmy angelfishes: discordance between taxonomy, coloration, and phylogenetics. Coral Reefs **13**, 839—851.

Drew, J. A. & Barber, P. H. 2012: Comparative phylogeography in Fijian coral reef fishes: a multi-taxa approach towards marine reserve design. PLoS One **7**, e47710.

Drew, J. & Kaufman, L. 2012: Functional endemism: population connectivity, shifting baselines, and the scale of human experience. Ecol. Evol. **3**, 450—456.

Drew, J., Allen, G. R., Kaufman, L. & Barber, P. H. 2008: Endemism and regional color and genetic differences in five putatively cosmopolitan reef fishes. Conserv. Biol. **22**, 965—975.

Drew, J. A., Allen, G. R. & Erdmann, M. V. 2010: Congruence between mitochondrial genes and color morphs in a coral reef fish: population variability in the Indo-Pacific damselfish Chrysiptera rex (Snyder, 1909). Coral Reefs **29**, 439—444.

Fisher, R. & Bellwood, D. R. 2002: The influence of swimming speed on sustained swimming performance of late-stage reef fish larvae. Mar. Biol. **140**, 801—807.

Froukh, T. & Kochzius, M. 2007: Genetic population structure of the endemic fourline wrasse (*Larabicus quadrilineatus*) suggests limited larval dispersal distances in the Red Sea. Mol. Ecol. **16**, 1359—1367.

Galarza, J. A., Carreras-Carbonell, J., Macpherson, E., Pascual, M., Roques, S., Turner, G. F. & Rico, C. 2009: The influence of oceanographic fronts and early-life-history traits on connectivity among littoral fish species. Proc. Natl Acad. Sci. USA **106**, 1473—1478.

Gerlach, G., Atema, J., Kingsford, M. J., Black, K. P. & Miller-sims, V. 2007: Smelling home can prevent dispersal of reef fish larvae. Proc. Natl Acad. Sci. USA **104**, 858—863.

Grutter, A. S. 1997: Spatiotemporal variation and feeding selectivity in the diet of the cleaner fish *Labroides dimidiatus*. Copeia **1997**, 346—355.

Grutter, A. S. 2012: Enhanced colonization success and competition associated with conspecifics in cleaner fish *Labroides dimidiatus* juveniles. Coral Reefs **31**, 1169—1176.

Grutter, A. S. & Bshary, R. 2004: Cleaner fish, *Labroides dimidiatus*, diet preferences for different types of mucus and parasitic gnathiid isopods. Anim. Behav. **68**, 583—588.

Igulu, M. M., Nagelkerken, I., Fraaije, R., Van Hintum, R., Ligtenberg, H. & Mgaya, Y. D. 2011: The potential role of visual cues for microhabitat selection during the early life phase of a coral reef fish (*Lutjanus fulviflamma*). J. Exp. Mar. Biol. Ecol. **401**, 118—125.

Jacoby, C. A. & Greenwood, J. G. 1988: Spatial, temporal, and behavioral patterns in emergence of zooplankton in the lagoon of Heron Reef, Great Barrier Reef. Australia. Mar. Biol. **97**, 309—328.

Jones, C. M. & Grutter, A. S. 2007: Variation in emergence of parasitic and predatory isopods among habitats at Lizard Island, Great Barrier Reef. Mar. Biol. **150**, 919—927.

Liu, S. Y. V., Dai, C. F., Allen, G. R. & Erdmann, M. V. 2012: Phylogeography of the neon damselfish *Pomacentrus coelestis* indicates a cryptic species and different species origins in the West Pacific Ocean. Mar. Ecol. Prog. Ser. **458**, 155—167.

Mahon, J. L. 1994: Advantage of flexible juvenile coloration in two species of *Labroides* (Pisces: Labridae). Copeia **1994**, 520.

Malek, T. B., Boughman, J. W., Dworkin, I. & Peichel, C. L. 2012: Admixture mapping of male nuptial colour and body shape in a recently formed hybrid population of threespine stickleback. Mol. Ecol. **21**, 5265—5279.

Mouritsen, H., Atema, J., Kingsford, M. J. & Gerlach, G. 2013: Sun compass orientation helps coral reef fish larvae return to their natal reef. PLoS One **8**, e66039.

Radford, C. A., Stanley, J. A., Simpson, S. D. & Jeffs, A. G. 2011: Juvenile coral reef fish use sound to locate habitats. Coral Reefs **30**, 295—305.

Raihani, N. J., Grutter, A. S. & Bshary, R. 2010: Punishers benefit from third-party punishment in fish. Science **327**, 171.

Raihani, N. J., Pinto, A. I., Grutter, A. S., Wismer, S. & Bshary, R. 2012: Male cleaner wrasses adjust punishment of female partners according to the stakes. Proc. Biol. Sci. **279**, 365—370.

Randall, J. E. 1958: A review of the Labrid fish genus *Labroides,* with desiccations of two new species and notes on ecology. Pacific Science **12**, 327—347.

Randall, J. E. 1981: Revision of the Labrid fish genus Labropsis with descriptions of five new species. Micronesica **17**, 125—155.

Randall, J. E. 2005: Reef and Shore Fishes of the South Pacific. Univ. of Hawaii Press, Honolulu, HI.

Robertson, D. R. & Hoffman, S. G. 1977: The roles of female mate choice and predation in the mating system of some tropical Labroid fishes. Zeitschrift fur Tierpsychologie **45**, 298—320.

Rocha, L. A., Robertson, D. R., Roman, J. & Bowen, B. W. 2005: Ecological speciation in tropical reef fishes. Proc. Biol. Sci. **272**, 573.

Rogers, S. M. & Bernatchez, L. 2007: The genetic architecture of ecological speciation and the association with signatures of selection in natural lake whitefish (*Coregonus* sp. Salmonidae) species pairs. Mol. Biol. Evol. **24**, 1423—1438.

Rogers, S. M., Mee, J. A. & Bowles, E. 2013: The consequences of genomic architecture on ecological speciation in postglacial fishes. Curr. Zool. **59**, 53—71.

Seehausen, O., Terai, Y., Magalhaes, I. S., Carleton, K. L., Mrosso, H. D. J., Miyagi, R., van der Sluijs, I., Schneider, M. V., Maan, M. E., Tachida, H., Imai, H. & Okada, N. 2008: Speciation through sensory drive in cichlid fish. Nature **455**, 620—626.

Sims, C. A., Riginos, C., Blomberg, S. P., Huelsken, T., Drew, J. & Grutter, A. S. 2014: Cleaning up the biogeography of *Labroides dimidiatus* using phylogenetics and morphometrics. Coral Reefs **33**, 223—233.

Taylor, M. S. & Hellberg, M. E. 2005: Marine radiations at small geographic scales: speciation in neotropical reef gobies (*Elacatinus*). Evolution **59**, 374—385.

Terry, A., Bucciarelli, G. & Bernardi, G. 2000: Restricted gene flow and incipient speciation in disjunct Pacific ocean and Sea of Cortez populations of a reef fish species, *Girella nigricans*. Evolution **54**, 652—659.

Treml, E. A., Roberts, J. J., Chao, Y., Halpin, P. N., Possingham, H. P. & Riginos, C. 2012: Reproductive output and duration of the pelagic larval stage determine seascape-wide connectivity of marine populations. Integr. Comp. Biol. **52**, 525—537.

Victor, B. C. 1986: Duration of the planktonic larval stage of one hundred species of Pacific and Atlantic wrasses (family Labridae). Mar. Biol. **90**, 317—326.

Warner, R. R. 1997: Evolutionary ecology: how to reconcile pelagic dispersal with local adaptation. Coral Reefs **16**, S115—S120.

Westneat, M. W. & Alfaro, M. E. 2005: Phylogenetic relationships and evolutionary history of the reef fish family Labridae. Mol. Phylogenet. Evol. **36**, 370—390.

Westneat, M. W., Alfaro, M. E., Wainwright, P. C., Bellwood, D. R., Grubich, J. R., Fessler, J. L., Clements, K. D. & Smith, L. L. 2005: Local phylogenetic divergence and global evolutionary convergence of skull function in reef fishes of the family Labridae. Proc. Biol. Sci. **272**, 993—1000.

Wismer, S., Pinto, A. I., Vail, A. L., Grutter, A. S. & Bshary, R. 2014: Variation in cleaner wrasse cooperation and cognition: influence of the developmental environment? Ethology **120**, 519—531.