Journal of the Ocean Science Foundation

2017, Volume 26



ARTICLE

Examples of symbiosis in tropical marine fishes

JOHN E. RANDALL

Bishop Museum, 1525 Bernice St., Honolulu, HI 96817-2704, USA E-mail: jackr@hawaii.rr.com

ARIK DIAMANT

Department of Pathobiology, Israel Oceanographic and Limnological Research Institute National Center of Mariculture, Eilat, Israel 88112 E-mail: diamant@ocean.org.il

Introduction

The word symbiosis is from the Greek meaning "living together", but present usage means two dissimilar organisms living together for mutual benefit. Ecologists prefer to use the term mutualism for this. The significance of symbiosis and its crucial role in coral reef function is becoming increasingly obvious in the world's warming oceans. A coral colony consists of numerous coral polyps, each like a tiny sea anemone that secretes calcium carbonate to form the hard skeletal part of coral. The polyps succeed in developing into a coral colony only by forming a symbiotic relationship with a free-living yellowish brown algal cell that has two flagella for locomotion. These cells penetrate the coral tissue (the flagella drop off) to live in the inner layer of the coral polyps collectively as zooxanthellae and give the yellowish brown color to the coral colony. As plants, they use the carbon dioxide and water from the respiration of the polyps to carry out photosynthesis that provides oxygen, sugars, and lipids for the growth of the coral. All this takes place within a critical range of sea temperature. If too warm or too cold, the coral polyps extrude their zooxanthellae and become white (a phenomenon also termed "bleaching"). If the sea temperature soon returns to normal, the corals can be reinvaded by the zooxanthellae and survive.

The current scientific community generally agrees that if the warming of our planet from the burning of fossil fuels continues, along with deforestation, our coral reefs are doomed. The corals of the magnificent Great Barrier Reef of Australia are beginning to die, and with them all the dependent marine life will likely perish. We should learn all we are able about the biology of coral reefs. A long list of relevant publications on the ecology of coral reefs, especially with respect to fishes, is given below in References. The following are among the more important papers that report on symbiosis on coral reefs, especially in relation to fishes: Ormond (1980a, 1980b), Diamant & Shpigel (1985), and Bshary *et al.* (2006).

Knowing that my colleague Arik Diamant in Israel has photographs of different species of fishes that forage together, as well as fishes with octopus, I suggested that we join forces and present the best photos we can find to illustrate symbiosis in fishes. We have assembled 27 photographs for this article.



The iconic symbiotic association that comes to a biologist's mind is often that of an anemonefish and its host sea anemone (Fig. 1). The advantage to the anemonefish is obvious; the stinging cells of the anemone tentacles dissuade a predaceous fish from trying to make a meal of the anemonefish (which is protected by a mucus that prevents the anemone's stinging cells from firing). But what is the advantage of the partnership to the anemone? Drop a small object, such as a shell fragment or piece of seagrass, onto its tentacles and see what happens— the anemonefish will promptly remove it. More important, there are predaceous fishes, notably species of the filefish family Monacanthidae and the striped butterflyfish *Chaetodon fasciatus* (Chaetodontidae), that feed on anemones. Despite their small size, anemonefishes usually succeed in driving such sea-anemone predators away.

Key words: mutualism, commensalism, ichthyology, ecology, coral-reef fishes, Indo-Pacific, undersea photography.

Citation: Randall, J.E. & Diamant, A. (2017) Examples of symbiosis in tropical marine fishes. *Journal of the Ocean Science Foundation*, 26, 95–115.

doi: http://dx.doi.org/10.5281/zenodo.579544



Figure 1. The Clown Anemonefish *Amphiprion ocellaris* Cuvier and its host, the Magnificent Sea Anemone *Heteractis magnifica* Quoy & Gaimard, photographed at Stephanie Island, Wayag Islands, Raja Ampat Regency, West Papua, Indonesia. The translucent whitish color of the tentacles of the anemone is the probable result of recent warming of the sea causing the expulsion of its zooxanthellae (J.E. Randall).

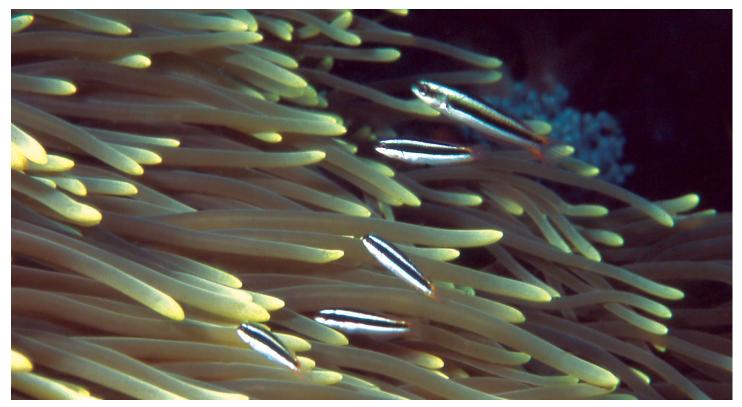


Figure 2. Five initial-phase Blunthead Wrasse, *Thalassoma amblycephalum* (Bleeker), appear to enjoy the same immunity from being stung by the tentacles of the large anemone, *Heteractis magnifica* (Quoy & Gaimard), as an anemonefish, at the island of Rinca in the Lesser Sunda Islands, Indonesia. Fautin & Allen (1992: 5) wrote that the wrasse makes only brief contact and is not dependent on the anemone. True, the wrasse is usually free-living, but its proximity to the anemone provides protection from predation, and it probably feeds on larval fishes and the larger invertebrates of the zooplankton that have been killed or adversely affected by contact with the anemone tentacles (J.E. Randall).



Figure 3. The three striped labrid fishes in the proximity of anemone tentacles were first identified as large individuals of the initial phase of *Thalassoma ambycephalum*. Noting the presence of a narrow ventral black stripe on the body and the more anterior orange coloration, we now believe it to be a possible new species of *Thalassoma*. The fourth wrasse is a juvenile *Thalassoma lunare* (Linnaeus). Photo taken at the Indonesian island of Rinca between Komodo and Flores (J.E. Randall).



Figure 4. The porcellanid crab *Neopetrolisthes maculatus* has been regarded as a commensal of large sea anemones (as by Colin & Arneson [1995], Gosliner *et al.* [1996], and Humann & DeLoach [2010]). However, the first author observed this one at the island of Ambon, Indonesia nipping off the tips of anemone tentacles, alternately with each cheliped, and taking them to its mouth. We therefore change its role with respect to the anemone as a parasite (J.E. Randall).



Figure 5. The Mushroom Coral *Heliofungia actiniformis* first develops on a coral reef, but detaches and becomes a solitary coral on the sea floor. It often harbors the slender white pipefish *Siokunichthys nigrolineatus* Dawson (to as many as nine), as in this photo from Ambon, Indonesia. The fish species name refers to the oblique line that passes through the eye; it is red, not black, in life. Bos (2011) cited seven different gobies and wrasses as occasional inquilines of the coral (J.E. Randall).



Figure 6. The Steephead Parrotfish *Chlorurus microrhinos* (Bleeker), photographed here at Enewetak Atoll, Marshall Islands, is in symbiotic association with coral. As an "excavator" parrotfish, this species bites deeply into the substrate. Only a portion of its diet is live coral, in general, most of its grazing is on algae (Bellwood & Choat 1990). It benefits the coral reef by removing algae that can kill coral by overgrowth. In addition, its powerful beak-like jaws bite into the limestone substratum, creating new surfaces for settlement of coral larvae. The ingested limestone fragments are ground into fine sand by its unique pharyngeal dentition, at the same time triturating the algae to make it more digestible. At some localities, such as the Cayman Islands, sheltered in the Caribbean Sea, most of the sand is created by parrotfishes (J.E. Randall).



Figure 7. An aggregation of the Bluegreen Chromis, *Chromis viridis* Cuvier in C. & V., on a colony of coral of the genus *Acropora*, photographed in the northern Red Sea. The coral provides shelter for the damselfish, and the excretions of the fish contain nutrients that are utilized by the coral (A. Diamant).

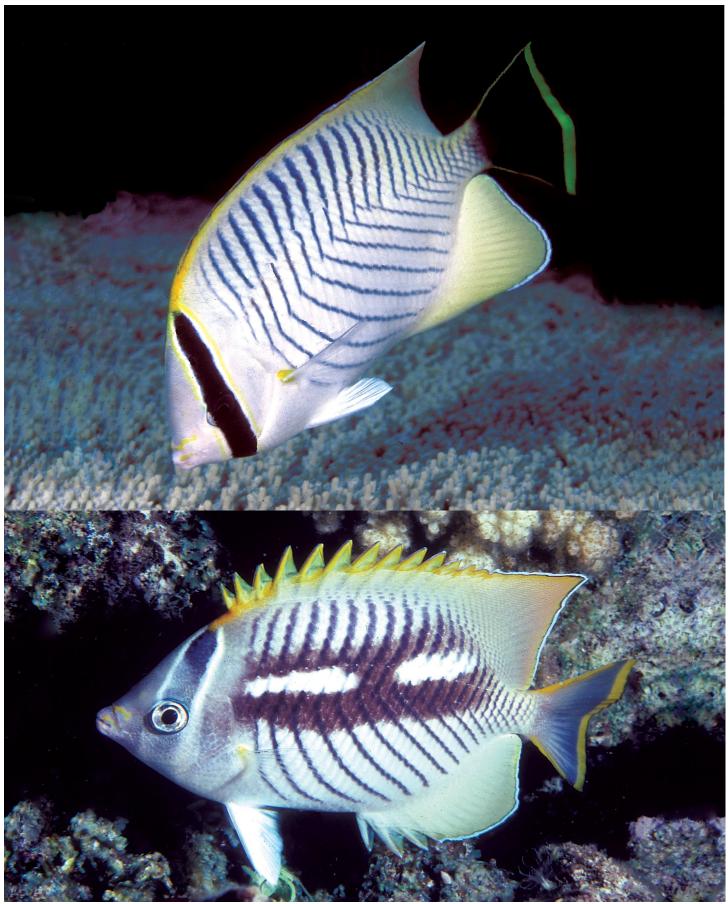


Figure 8. The Chevron Butterflyfish, *Chaetodon trifascialis* Quoy & Gaimard, photographed at Johnston Island during the day (upper) and at Enewetak Atoll, Marshall Islands at night (lower), feeds on polyps of coral of the genus *Acropora*. The species was formerly classified in the genus *Megaprotodon*, now a subgenus. It is the most aggressive species of the genus in protecting its private territory of live coral from other coral-feeding species of fishes (J.E. Randall).



Figure 9. The Blackmargin Damselfish, *Dascyllus marginatus* (Rüppell), is symbiotic with the coral *Stylophora pistillata* in the Red Sea (also reported from Oman). It nestles among branches of the coral an average of 26% of the time during the day, and all of the night. Its excretions include nutrients rich in nitrogen and phosphorus that are utilized by the coral. The fish removes debris from the coral, helps facilitate water turnover between the branches, and protects it from coral-feeding fishes, such as species of *Chaetodon*, as well as the Crown-of-Thorns Starfish, *Acanthaster planci*. Coral colonies inhabited by fish grow faster and produce more ova than coral without associated fish (Garcia-Herrera *et al.* 2017). In the lower part of the coral, where the damselfish resides at night, a low level of oxygen is prevented by current created from vigorous movements of its fins while the fish remains stationary (Goldschmid *et al.* 2004) (J.E. Randall).



Figure 10. The Lined Triplefin, *Helcogramma striatum* Hansen, photographed here in the Ogasawara Islands of Japan, resides symbiotically with live coral. It ranges from Sri Lanka to Fiji. It is one of a multitude of small fishes that may be found on live coral, including other tripterygiids of the genera *Ceratobregma*, *Enneapterygius*, *Norfolkia*, *Springerichthys* and *Ucla*; gobies of the genera *Bryaninops*, *Discordipinna*, *Eviota* (112 species at present), *Gobiodon*, *Paragobiodon*, *Pleurosicya*, *Priolepis*, and *Trimma*. Some blennies of the genera *Atrosalarias*, *Cirripectes*, *Ecsenius*, *Meiacanthus*, and *Petroscirtes* are coral inquilines, and *Exallias brevis* feeds on coral (J.E. Randall).



Figure 11. The diminutive Speckled Scorpionfish, *Sebastapistes coniorta* Jenkins, is typically found well hidden among the branches of *Pocillopora meandrina*; the largest specimen of the fish is only 9.4 cm. Endemic to the Hawaiian Islands and Johnston Island (this photo from Kona, Hawaii). Feeds mainly at night on benthic crustaceans (J.E. Randall).

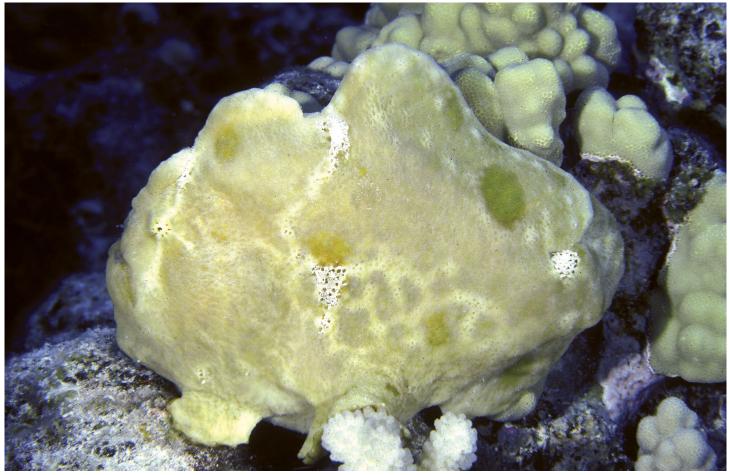


Figure 12. The frogfish *Antennarius commerson* (Latreille), photographed in Kona, Hawai'i, is obviously a long-term resident of this colony of *Porites lobata* (note the posterior gap that it normally fills); one pelvic fin leans on the tip of a branch of *Pocillopora meandrina*. This species can also be totally bright yellow, nearly totally red or black, or variously mottled. It is wide-ranging in the Indo-Pacific, and is reported from the tropical eastern Pacific (J.E. Randall).



Figure 13. The juvenile (upper) and adult (lower) of the Blackside Hawkfish, *Paracirrhites forsteri* (Bloch & Schneider) are nearly always found in close association with live coral, more in outer reef than protected reef areas; ranges throughout the Indo-Pacific region from the Red Sea and East Africa to the Hawaiian Islands and Pitcairn Islands; in the western Pacific from New South Wales to Japan. Feed mainly on fishes, occasionally on crustaceans (J.E. Randall).

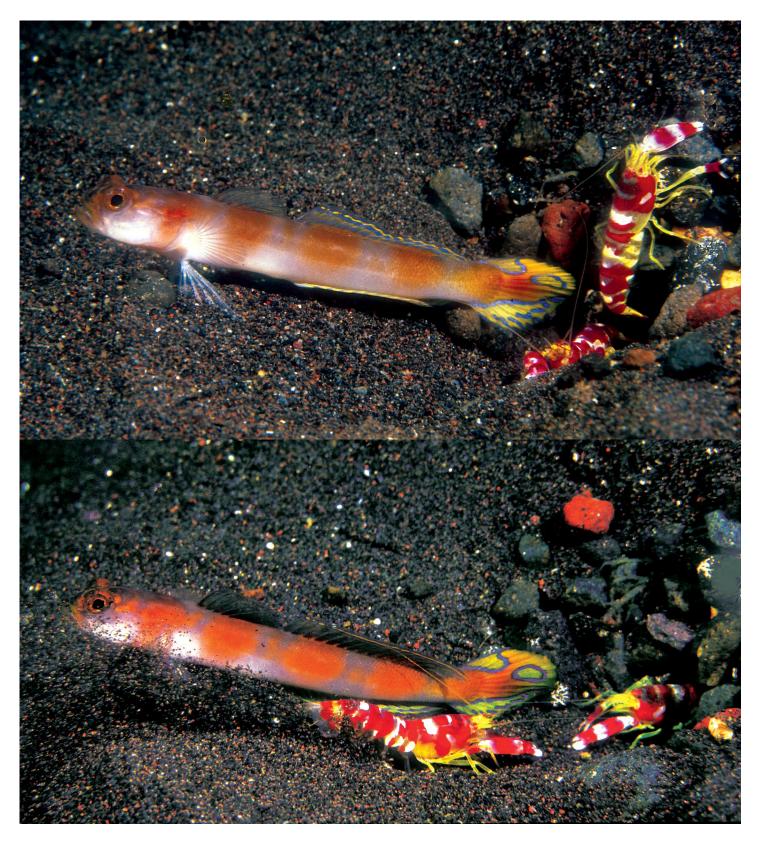


Figure 14. The goby *Amblyeleotris yanoi* Aonuma & Yoshino and its symbiotic partner, the snapping shrimp *Alpheus randalli* Banner & Banner, in Bali, Indonesia. The shrimps, usually found in a male-female pair, construct and maintain a burrow that is shared with the goby. The latter, with its superior vision and lateral-line sensory system, serves as the sentinel. The lower photograph, taken the next day, shows one shrimp sending sand flying away from the surplus near the burrow entrance by the action of its swimmerets (J.E. Randall).



Figure 15. This Green Sea Turtle, *Chelonia mydas* (Linnaeus), in Puako, Hawai'i, swam to a group of Yellow Tang, *Zebrasoma flavescens* (Bennett), that proceeded to feed on algae growing on the turtle, especially the neck, where it must have impeded movement of its head. If allowed to grow unchecked, the algae will slow the swimming speed of the turtle and make it more vulnerable to predation. We wonder why we see so little algae and other marine growth on the turtle's carapace, suggesting that it is so smooth that a coral larva or algal spore may have difficulty attaching (M. Roberts).



Figure 16. A Green Sea Turtle, *Chelonia mydas* (Linnaeus), in Negros, Philippines, being "cleaned" by the damselfish *Pomacentrus brachialis* Cuvier in C. & V. (C. Holdt).



Figure 17. This Big Blue Octopus, *Octopus cyanea* Gray, observed in the Gulf of Oman, is probably having skin parasites removed by the damselfish *Neopomacentrus miryae* Dor & Allen (J.E. Randall).



Figure 18. The Scalloped Hammerhead, *Sphyrna lewini* (Griffith & Smith), at Cocos Island, Costa Rica, having its external parasites removed by a trio of King Angelfish, *Holacanthus passer* Valenciennes (A. Klapfer).

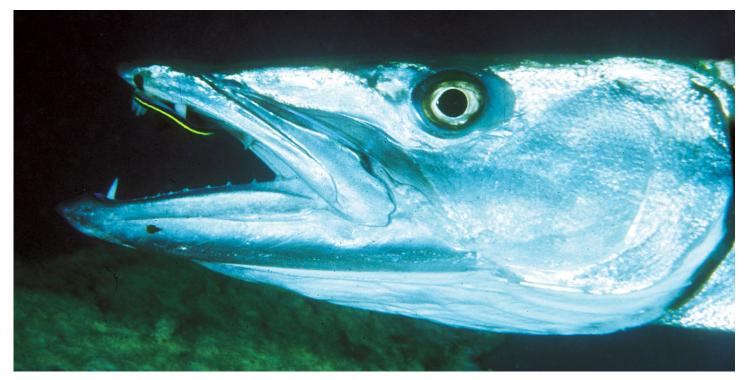


Figure 19. This meter-long Great Barracuda, *Sphyraena barracuda* (Edwards), swam within touching distance of the photographer enroute to a shallow reef of the marine reserve at Bonaire, where it opened its mouth. A Yellownose Goby, *Elacatinus randalli* (Böhlke & Robins), accepted the invitation and swam to the jaws, where it commenced feeding on ectoparasites (chiefly larval gnathiid isopods). The two calagid copepods attached anteriorly on the side of both jaws appear too large to be prey for the cleaning goby (J.E. Randall).



Figure 20. The grouper *Plectropomus leopardus* (Lacépède) having parasites removed by a pair of Cleaner Wrasses, *Labroides dimidiatus* (Valenciennes in C. & V.), at Heron Island on the Great Barrier Reef of Australia (J.E. Randall).



Figure 21. Two goatfish, *Parupeneus cyclostomus* (Lacépède), the emperor *Lethrinus microdon* Valenciennes in C. & V., the snapper *Lutjanus decussatus* (Cuvier in C. & V.), and the jack *Caranx melampygus* Cuvier in C. & V. foraging together near the wreck of the ASAT *Liberty* in Bali, Indonesia (J.E. Randall).



Figure 22. The Greasy Grouper, *Epinephelus tauvina* (Forsskål), and the Grey Moray, *Gymnothorax griseus* (Lacépède), foraging together in the northern Red Sea. Physical contact between the partners is frequent (A. Diamant).



Figure 23. A Big Blue Octopus, *Octopus cyanea* Gray, is seen here as it forages in the northern Red Sea, closely tailed by two goatfishes, *Parupeneus cyclostomus* and *P. macronema*, both described by Lacépède, and a Blacktip Grouper, *Epinephelus fasciatus* (Forsskål). In this symbiosis of cooperative foraging, hidden prey trying to escape the probing tentacles of the octopus are often captured by the highly attentive fishes, which, in turn, discourage prey from fleeing the crevices as the octopus approaches. The octopus feeds mainly on gastropods and pelecypods, but occasionally captures small fishes (A. Diamant).



Figure 24. Two species of groupers, the drab Redmouth Grouper, *Aethaloperca rogaa*, and the blue-spotted Coral Hind, *Cephalopholis mineata*, both described by Forsskål, have converged with the Yellow-edged Moray *Gymnothorax flavimarginatus* (Rüppell) to prey on the Lyretail Anthias *Pseudanthias squamipinnis* (Peters) in the northern Red Sea. Some color of the Anthias prey may be seen between the two Coral Hinds; a second Redmouth Grouper is visible only by part of the caudal fin at the upper left (A. Diamant).

Epilogue

Remembering our success in saving the American Bison and the California Condor from extinction, we should endeavor to do the same for threatened endemic marine fishes and invertebrates. Support should be provided to rear endemic marine life in aquaria. The State of Hawai'i should be among the first to consider such a conservation project. Twenty-five percent of the reef and shore fishes of the Hawaiian Islands are endemic, the highest proportion for any island region in the world. Hawai'i's most widely exported reef fish, the Yellow Tang (*Zebrasoma flavescens*), though not endemic, has been successfully reared from the egg, as has a wide variety of other families of reef fishes. The Hawai'i Larval Fish Project by Frank Baensch's Reef Culture Technologies has now successfully cultured 37 species of Hawaiian fishes (http://www.rcthawaii.com).

Acknowledgments

The authors thank Christa Holdt, Michael Roberts, and Avi Klapfer for their exceptional photographs that illustrate symbiosis in the sea. Comments by Arthur Bos, Mark Hixon, Robert Myers, and Rupert Ormond are greatly appreciated. We are indebted to Mark Hixon and Helen A. Randall for assistance with references. We are most grateful to the editor, Benjamin C. Victor, who declined our invitation to join as an author, in view of his substantial contribution to the paper.

References & Literature

- Abel, E. (1960) Zur kenntnis des Verhaltens und der Ökologie von Fischen an korallenriffen bei Ghardaqa (Rotes Meer). *Zeitschrift für Morphologie und Ökologie der Tiere*, 49, 430–539.
- Al-Hussaini, A.H. (1947) The feeding habits and the morphology of the alimentary tract of some teleosts living in the neighborhood of the Marine Biological Station, Ghardaqa, Red Sea. *Publications of the Marine Biological Station, Ghardaqa, Red Sea*, 5, 1–61.
- Almany, G.R.. Berumen, M.L., Thorrold, S.R., Planes, S. & Jones, G.P. (2007) Local replenishment of coral reef fish populations in a marine reserve. *Science*, 316, 742–744.
- Anderson, G.R.V., Ehrlich, A.H., Ehrlich, P.R., Roughgarden, J.D., Russell, B.C. & Talbot, F.H. (1981) The community structure of coral reef fishes. *The American Naturalist*, 117, 476–495.
- Bailey, T.G. & Robertson, D.R. (1982) Organic and caloric levels of fish feces relative to its consumption by coprophagous reef fishes. *Marine Biology*, 69, 45–50.
- Bakus, G.J. (1969) Effects of the feeding habits of coral reef fishes on the benthic biota. *In*: Mukundan, C. & Gopindha Pillai, C.S. (Eds.) *Proceedings of the First International Symposium on Corals and Coral Reefs*, Marine Biological Association of India, Mandapam Camp, India, pp. 445–448.
- Bellwood, D.R. (1998) What are reef fishes?-- Comment on the report by D.R. Robertson: Do coral-reef fish faunas have a distinctive taxonomic structure? *Coral Reefs*, 17, 179–186
- Bellwood, D.R. & Choat, J.H. (1990) A functional analysis of grazing in parrotfishes (family Scaridae): the ecological implications. *Environmental Biology of Fishes*, 28: 189–214. http://dx.doi.org/10.1007/BF00751035 Birkeland, C. (1997) *Life and Death of Coral Reefs*. Chapman & Hall, New York, NY, USA, 536 pp.
- Bos, A.R. (2012) Fishes (Gobiidae and Labridae) associated with the mushroom coral *Heliofungia actiniformis* (Scleractinia: Fungiidae) in the Philippines. *Coral Reefs*, 31, 133.
- Bos, A.R. & Hoeksma, B.W. (2015) Cryptobenthic fishes and co-inhabiting shrimps associated with the mushroom coral *Heliofungia actiniformis* (Fungiidae) in the Davao Gulf, Philippines. *Environmental Biology of Fishes*, 98 (6), 1479–1489.
- Bos, A.R. & Hoeksma, B.W. (2017) Mushrooom corals (Fungiidae) and their associated fauna in the Davao Gulf, Philippines. *The Raffles Bulletin of Zoology*, (in press).
- Brock, R.E., Lewis, C. & Wass, R.C. (1979) Stability and structure of a fish community on a coral patch reef in Hawaii. *Marine Biology*, 54, 281–292.
- Brothers, E.B., Williams, D.M. & Sale, P.F. (1983) Length of larval life in twelve families of fishes of "One Tree Lagoon", Great Barrier Reef, Australia. *Marine Biology*, 76, 319–324.
- Bshary, R., Hohner, A., Ait-el-Djoudi, K. & Fricke, H. (2006) Interspecific communicative and coordinated hunting between groupers and giant moray eels. *PLoS Biology*, 4 (12), e431. https://doi.org/10.1371/journal.pbio.0040431
- Buckley, R.M., West, J.E. & Doty, D.C. (1994) Internal micro-tag systems for marking juvenile reef fishes. *Bulletin of Marine Science*, 55, 848–857.
- Ceccarelli, D.M., Jones, G.P. & McCook, L.J. (2005) Foragers versus farmers: contrasting effects of two behavioural groups of herbivores on coral reefs. *Oecologia*, 145, 445–453.
- Chave, E.H. & Randall, H.A. (1971) Feeding behavior of the moray eel *Gymnothorax pictus*. *Copeia*, 1971, 570–574.
- Choat, J.H. & Robertson, D.R. (1975) Protogynous hermaphroditism in fishes of the family Scaridae. *In*: Reinboth, R. (Ed.) *Intersexuality in the animal kingdom*. Springer-Verlag, Heidelberg, Germany, pp. 263–283.
- Coles, S.L. (1984) Colonization of Hawaiian reef corals on new and denuded substrata in the vicinity of a Hawaiian power station. *Coral Reefs*, 3, 123–130.
- Colin, P.L. & Arneson, C. (1995) *Tropical Pacific Invertebrates*. Coral Reef Press, Beverly Hills, CA, USA, vii + 295 pp.
- Collette, B.B. & Talbot, F.H. (1972) Activity patterns of coral fishes with emphasis on nocturnal-diurnal changeover. *In: Results of the Tektite Program, Ecology of Coral Reef Fishes. Bulletin of the Natural History Museum, Los Angeles*, 14, pp. 98–124.
- Côté, I.M. & Reynolds. J.D. (2006) *Coral Reef Conservation*. Cambridge University Press, Cambridge, UK, 568 pp. Diamant, A. & Shpigel, M. (1985) Interspecific feeding associations of groupers (Teleostei: Serranidae) with octopuses and moray eels in the Gulf of Eilat (Aqaba). *Environmental Biology of Fishes*, 13 (2), 153–159.

- Doherty, P.J. & Sale, P.F. (1985) Predation on juvenile coral reef fishes: an exclusion experiment. *Coral Reefs*, 4, 225–234.
- Domeier, M.L. & Colin, P.L. (1997) Tropical reef spawning aggregations defined and reviewed. *Bulletin of Marine Science*, 60, 698–726.
- Ebersole, J.P. (1977) The adaptive significance of interspecific territoriality in the reef fish *Eupomacentrus leucostictus*. *Ecology*, 58, 914–920.
- Edmondson, C.H. (1928) The ecology of a Hawaiian coral reef. *Bulletin of the Bernice P. Bishop Museum*, 45, 1–64
- Ehrlich, P.R. (1975) The population biology of coral reef fishes. *Annual Review of Ecology and Systematics*, 6, 211–234.
- Eibl-Eibesfeldt, I. (1955) Über Symbiosen, Parasitismus und andere besondere zwischenartliche Beziehungen tropischer Meeresfische. *Zeitschrift für Tierpsychologie*, 12, 203–219. doi:10.1111/j.1439-0310.1955. tb01523.x
- Fautin, D.G. (1991) The anemonefish symbiosis: what is known and what is not. *Symbiosis*, 10, 23–46.
- Fautin, D.G. & Allen, G.R. (1992) *Field Guide to Anemonefishes and their Host Sea Anemones*. Western Australian Museum, Perth, Australia, vi + 158 pp.
- Fishelson, L. (1977) Sociobiology of feeding behavior of coral fish along the coral reef of the Gulf of Eilat, Red Sea. *Israel Journal of Zoology*, 26, 114–134.
- Fishelson, L., Popper, D. & Avidor, A. (1974) Biosociology and ecology of pomacentrid fishes around the Sinai peninsula (Northern Red Sea). *Journal of Fish Biology*, 6, 119–133.
- Fricke, R.W. (1977) Community structure, social organisation and ecological requirements of coral reef fish (Pomacentridae). *Helgoländer Wissenschaftliche Meersunters*, 10, 412–426.
- Garcia-Herrera, N., Ferse, C.A., Kunzmann, A. & Genin, A. (2017) Mutualistic damselfish induce higher photosynthetic rates in their host coral. *Journal of Experimental Biology*, 220, 1803–1811.
- Garrison, G. (2005) *Peces de la Isla del Coco. Segunda Edición*. Instituto Nacional de Biodiversidad, Costa Rica, 430 pp.
- Glynn, P.W., Cortes, J., Guzman, H.M. & Richmond, R.H. (1988) El Nino (1982–83) associated coral mortality and relationship to sea surface temperature devations in the tropical eastern Pacific. *In*: Choat, J.H. *et al.* (Eds.) *Proceedings of the 6th International Coral Reef Symposium: Vol. 3: Contributed Papers*. Townsville, Australia, pp. 237–243.
- Glynn, P.W., Stewart, R.H. & McCosker, J.E. (1972) Pacific coral reefs of Panama: structure, distribution and predators. *Geologische Rundschau*, 61, 483–519.
- Goldschmid, R., Holzman, R., Weihs, D. & Genin, H. (2004) Aeration of corals by sleep-swimming fish. *Limnology and Oceanography*, 45, 1832–1859.
- Gosline, W.A. (1965) Vertical zonation of inshore fishes in the upper water layers of the Hawaiian Islands. *Ecology*, 46, 823–831.
- Gosliner, T.M., Behrens, D.W. & Williams, G.C. (1996) *Coral Reef Animals of the Indo-Pacific*. Sea Challengers, Monterey, CA., USA, vi + 314 pp.
- Grutter, A.S. (1997) Effect of the removal of cleaner fish on the abundance and species composition of reef fish. *Oecologia*, 111, 137–143.
- Grutter, A.S. (1999) Cleaner fish really do clean. *Nature*, 398, 672–673.
- Grutter, A.S., Murphy, J.M. & Choat, J.H. (2003) Cleaner fish drives local fish diversity on coral reefs. *Current Biology*, 13, 64–67.
- Harmelin-Vivien, M.L. & Bouchon, C. (1976) Feeding behavior of some carnivorous fishes (Serranidae and Scorpaenidae) from Tuléar (Madagascar). *Marine Biology*, 37, 329–340.
- Harmelin-Vivien, M.L. & Bouchon-Navaro, Y. (1983) Feeding diets and significance of coral feeding among chaetodontid fishes in Moorea (French Polynesia). *Coral Reefs*, 2, 119–127.
- Harriott, V.J. (1985) Mortality rates of scleratinian corals before and during a mass bleaching event. *Marine Ecology Progress Series*, 21, 81–88.
- Hay, M.E. & Taylor, P.R. (1985) Competition between herbivorous fishes and urchins on Caribbean reefs. *Oecologia*, 65, 591–598.
- Helfman, G.S. (1978) Patterns of community structure in fishes: summary and overview. *Environmental Biology of Fishes*, 3, 129–148.

- Hiatt, R.W. & Strasburg, D.W. (1960) Ecological relationships of fish fauna on coral reefs of the Marshall Islands. *Ecological Monographs*, 30, 65–127.
- Hixon, M.A. (2011) 60 years of coral reef fish ecology: past, present, future. *Bulletin of Marine Science*, 87, 727–765.
- Hixon, M.A. & Beets, J.P. (1993) Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecological Monographs*, 63, 77–101.
- Hixon, M.A., Boersma, P.D., Hunter, M.L., Micheli, F., Norse, E.A., Possingham, H.P. & Snelgrove, P.V.R. (2001) Oceans at risk: research priorities in marine conservation biology. *In*: Soulé, M.E. & Orians, G.H. (Eds.) *Conservation Biology: Research Priorities for the Next Decade*. Island Press, Washington, DC, USA, pp. 125–154.
- Hixon, M.A. & Brostoff, W.N. (1996) Succession and herbivory: effects of differential fish grazing on Hawaiian coral-reef algae. *Ecological Monographs*, 66, 67–90.
- Hoegh-Guldberg, O., Mumby, P.J., Hooten, A.J., Steneck, R.S., Greenfield, P., Gomez, E., Harvell, C.D., Sale, P.E., Edwards, A.J., Caldeira, K. *et al.* (2007) Coral reefs under rapid climate change and ocean acidification. *Science*, 318, 1737–1741.
- Humann, P. & DeLoach, N. (2010) *Reef Creature Identification, Tropical Pacific*. New World Publications, Jacksonville, FL., USA, 497 pp.
- Karplus, I. (1978) A feeding association between the grouper (*Epinephelus fasciatus*) and the moray eel (*Gymnothorax griseus*). *Copeia*, 1978, 164.
- Johannes, R.E. (1981) Words of the Lagoon: Fishing and Marine Lore in the Palau District of Micronesia. University of California Press, Berkeley, CA, USA, xiv + 245 pp.
- Jokiel, P. & Coles. S.L. (1990) Response of Hawaiian and other Indo-Pacific reef corals to elevated temperature. *Coral Reefs*, 8, 155–162.
- Jones, R.S. (1968) Ecological relationships in Hawaiian and Johnston Island Acanthuridae (surgeonfishes). *Micronesica*, 4, 309–361.
- Leis, J.M. (1986) Vertical and horizontal distribution of fish larvae near coral reefs at Lizard Island, Great Barrier Reef. *Marine Biology*, 90, 505–516.
- Longley, W.H. & Hildebrand, S.F. (1941) Systematic Catalogue of the Fishes of Tortugas, Florida, with Observations on Color, Habits, and Local Distribution. *Carnegie Institution of Washington Publication*, 535 (*Papers from Tortugas Laboratory*, vol. 34), 1–331.
- Losey, G.S. (1972) The ecological importance of cleaning symbiosis. *Copeia*, 1972, 820–831.
- Lorenz, K. (1962) The function of colour in coral reef fishes. *Proceedings of the Royal Institution*, 39, 282–296.
- MacArthur, R.H. (1972) Geographical Ecology: Patterns in the Distribution of Species. Harper & Row, New York, NY, USA, xviii + 269 pp.
- McLeod, E., Salm, R., Green, A. & Almany, J. (2009) Designing marine protected area networks to address the impacts of climate change. *Frontiers in Ecology and the Environment*, 7, 362–378.
- Mora, C. (2015) (Ed.) *Ecology of Fishes on Coral Reefs*. Cambridge University Press, Cambridge, UK, xiv + 374 pp.
- Morrison, D. (1988) Comparing fish and urchin grazing in shallow and deeper coral reef algal communities. Ecology, 69, 1367–1382.
- Myrberg, A.A. & Thresher, R.E. (1974) Interspecific aggression and its relevance to the concept of territoriality in reef fish. *American Zoologist*, 14, 81–96.
- Odum, H.T. & Odum, E.P. (1955) Trophic structure and productivity of a windward coral reef community of Enewetak Atoll. *Ecological Monographs*, 25, 291–330.
- Ogden, J.C. & Ebersole, J.P. (1981) Scale and community structure of coral reef fishes: a long-term study of a large artificial reef. *Marine Ecology Progress Series*, 4, 97–103.
- Ollerton, J., McCollin, D., Fautin, D.G. & Allen, G.R. (2007) Finding NEMO: nestedness engendered by mutualistic organization in anemonefish and their hosts. *Proceedings of the Royal Society B*, 274, 591–598
- Ormond, R.F.G. (1980a) Occurrence and feeding behavior of Red Sea coral reef fishes. *Proceedings of Symposium on the Coastal and Marine Environment of the Red Sea, Gulf of Aden and Tropical Western Indian Ocean, Khartoum, 9–14 January 1980*, 2, 329–371.
- Ormond, R.F.G. (1980b) Aggressive mimicry and other interspecific feeding associations among Red Sea coral reef predators. *Journal of the Zoological Society of London*, 191, 247–262.

- Planes, S., Galzin, R. & Bonhomme, F. (1996) A genetic metapopulation model for reef fishes in oceanic islands: the case of the surgeonfish, *Acanthurus triostegus*. *Journal of Evolutionary Biology*, 9, 103–117.
- Poulin, R. & Grutter, A.S. (1996) Cleaning symbioses: proximate and adaptive explanations. *BioScience*, 46, 512–517.
- Pratchett, M.S., Munday, P.I., Wilson, S.K., Graham, N.A.J., Cinner, J.E., Bellwood, D.R., Jones, G.P., Polunin, N.V.C. & McClanahan, T.R. (2008) Effects of climate-induced coral bleaching on coral reef fishes: ecological and economic consequences. *Oceanography and Marine Biology, Annual Review*, 46, 251–296.
- Randall, J.E. (1958) A review of ciguatera, a tropical fish poisoning with a tentative explanation of its cause. *Bulletin of Marine Science of the Gulf and Caribbean*, 8, 236–267.
- Randall, J.E. (1961) Overgrazing of algae by herbivorous marine fishes. *Ecology*, 42, 812.
- Randall, J.E. (1961) A contribution to the biology of the convict surgeon fish of the Hawaiian Islands, *Acanthurus triostegus sandvicensis*. *Pacific Science*, 15, 215–272.
- Randall, J.E. (1963) An analysis of the fish populations of artificial and natural reefs in the Virgin Islands. *Caribbean Journal of Science*, 3, 31–47.
- Randall, J.E. (1965) Grazing effects on seagrasses by herbivorous reef fishes in the West Indies. *Ecology*, 46, 255–260.
- Randall, J.E. (1967) Food habits of reef fishes of the West Indies. *Studies in Tropical Oceanography, University of Miami Institute Marine Science*, 5, 665–847.
- Randall, J.E. (1968) Caribbean Reef Fishes. TFH Publications, Neptune City, NJ, USA, 305 pp.
- Randall, J.E. (1974) The effect of fishes on coral reefs. *In*: A.M. Cameron *et al.* (Eds.) *Proceedings of the Second International Symposium on Coral Reefs, Vol. 1*, Great Barrier Reef Committee. Brisbane, Australia, pp. 159–166.
- Randall, J.E. (2005) A review of mimicry in marine fishes. Zoological Studies, 44, 299–328.
- Randall, J.E. (2007) *Reef and Shore Fishes of the Hawaiian Islands*. Sea Grant College Program, University of Hawai'i, Honolulu, HI, USA, xiv + 546 pp.
- Randall, J.E. & Brock, V.E. (1960) Observations on the ecology of epinepheline and lutjanid fishes of the Society Islands, with emphasis on food habits. *Transactions of the American Fisheries Society*, 89, 9–16.
- Randall, J.E. & Randall, H.A. (1960) Examples of mimicry and protective resemblance in tropical marine fishes *Bulletin of Marine Science of the Gulf and Caribbean*, 10, 444–480.
- Reese, E.S. (1975) A comparative field study of the social behavior and related ecology of reef fishes of the family Chaetodontidae. *Zeitschrift für Tierpsychologie*, 37, 37–61.
- Reese, E.S. (1977) Co-evolution of corals and feeding fishes of the family Chaetodontidae. *In*: D.L. Taylor (Ed.) *Proceedings of Third International Coral Reef Symposium Vol. 1: Biology.* Rosenstiel School of Marine and Atmospheric Science, Miami, FL, USA, pp. 267–274.
- Reese, E.S. (1981) Predation on corals by fishes of the family Chaetodontidae: implications for conservation and management of coral reef ecosystems. *Bulletin of Marine Science*, 31, 594–604.
- Roberts, C.M., Bohnsack, J.A., Gell, F., Hawkins, J.P. & Goodridge, R. (2011) Effects of marine reserves on adjacent fisheries. *Science*, 294, 1920–1923.
- Robertson, D.R. (1970) Review of the predators and parasites of stony corals, with special reference to symbiotic prosobranch gastropods. *Pacific Science*, 24, 43–54.
- Robertson, D.R. & Choat, J.H. (1974) Protogynous hermaphroditism and social systems in labrid fishes. *In*: A.M. Cameron *et al.* (Eds.) *Proceedings of the Second International Symposium on Coral Reefs, Vol. 1*, Great Barrier Reef Committee, Brisbane, Australia, pp. 217–225.
- Robertson, D.R. & Polunin, V.C. (1981) Coexistence: symbiotic sharing of feeding territories and algal food by some coral reef fishes from the Western Indian Ocean. *Marine Biology*, 62, 185–195.
- Robertson, D.R., Sweatman, H.P.A., Fletcher, E.A. & Cleland, M.G. (1976) Schooling as a mechanism for circumventing the territoriality of competitors. *Ecology*, 57, 1208–1220.
- Robertson, D.R. & Warner, R.R. (1978) Sexual patterns in the labroid fishes of the western Caribbean, II: The parrotfishes (Scaridae). *Smithsonian Contributions to Zoology*, 255, pp. 1–26.
- Roughgarden, J. & Feldman, M. (1975) Species packing and predation pressure. *Ecology*, 56, 489–492.
- Russ, G.R. & Alcala, A.C. (1996) Do marine reserves export adult fish biomass? Evidence from Apo Island, central Philippines. *Marine Ecology Progress Series*, 132, 1–9.

- Russell, B.C, Talbot, F.H. & Domm, S. (1974) Patterns of colonisation of artificial reefs by coral reef fishes. *In*: A.M. Cameron *et al.* (Eds.) *Proceedings of the Second International Symposium on Coral Reefs, Vol. 1*, Great Barrier Reef Committee, Brisbane, Australia, pp. 207–215.
- Sadovy, Y., Kulbicki, M., Labrosse, P., Letourneur, Y., Lokani, P. & Donaldson, T.J. (2003) The humphead wrasse, *Cheilinus undulatus*: synopsis of a threatened and poorly known giant coral reef fish. *Reviews in Fish Biology and Fisheries*, 13, 327–364.
- Sale, P.F. (1975) Patterns of use of space in a guild of territorial reef fishes. *Marine Biology*, 29, 89–97.
- Sale, P.F. (1978) Coexistence of coral reef fishes a lottery for living space. *Environmental Biology of Fishes*, 3, 85–102.
- Sale, P.F. (1980) The ecology of fishes on coral reefs. *Oceanography and Marine Biology, Annual Review*, 18, 367–421.
- Sale, P.F. (2002) (Ed.) *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem*. Academic Press, San Diego, CA, USA, 549 pp.
- Sale, P.F. & Dybdahl, R. (1975) Determinants of community structure for coral reef fishes in an experimental habitat. *Ecology*, 56, 1343–1355.
- Shapiro, D.Y. (1978) The structure and growth of social groups of the hermaphroditic fish *Anthias squamipinnis* (Peters). *In*: D.L. Taylor (Ed.) *Proceedings of Third International Coral Reef Symposium Vol. 1: Biology.* Rosenstiel School of Marine and Atmospheric Science, Miami, FL, USA, pp. 571–577.
- Shpigel, M. (1980) Niche overlap among two species of the genus *Dascyllus* (Pomacentridae). *Environmental Biology of Fishes*, 7, 65–68.
- Shpigel, M. & Fishelson, L. (1991) Experimental removal of piscivorous groupers of the genus *Cephalopholis* (Serranidae) from coral habitats in the Gulf of Aqaba (Red Sea). *Environmental Biology of Fishes*, 31, 131–138.
- Smith, C.L. & Tyler, J.C. (1972) Space resource sharing in a coral reef fish community. *Bulletin of the Natural History Museum of Los Angeles County, Science*, 14, 125–178.
- Starck, W.A. & Davis, W.P. (1966) Night habits of fishes at Alligator Reef, Florida. *Ichthyologica*, 38, 313–356.
- Talbot, F.H., Russell, B.C. & Anderson, G.R.V. (1978) Coral reef fish communities: unstable, high-diversity systems. *Ecological Monographs*, 48, 425–440.
- Thresher, R.E. (1984) Reproduction in Reef Fishes. TFH Publications, Neptune City, NJ, USA, 399 pp.
- Victor, B.C. (1986) Duration of the planktonic larval stage of one hundred species of Pacific and Atlantic wrasses (family Labridae). *Marine Biology*, 90, 317–326.
- Vine, P.J. (1974) Effects of algal grazing and aggressive behavior of the fishes *Pomacentrus lividus* and *Acanthurus sohal* on coral-reef ecology. *Marine Biology*, 24, 131–136.
- Walsh, W.I. (1983) Stability of a coral reef fish community following a catastrophic storm. *Coral Reefs*, 2, 49–63. Waldie, P.A., Blomberg, S.P., Cheney, K.L., Goldizen, A.W. & Grutter, A.S. (2011) Long-Term Effects of the
- Cleaner Fish *Labroides dimidiatus* on Coral Reef Fish Communities. PLoS ONE 6(6): e21201. https://doi. org/10.1371/journal.pone.0021201
- Warner, R.R. & Hughes, T.P. (1988) The population dynamics of reef fishes. *In*: Choat, J.H. *et al.* (Eds.) *Proceedings of the 6th International Coral Reef Symposium: Vol. 3: Contributed Papers*. Townsville, Australia, pp. 149-155.
- Wellington, G.M. & Victor, B.C. (1989) Planktonic larval duration of one hundred species of Pacific and Atlantic damselfishes (Pomacentridae). *Marine Biology*, 101, 557–567.
- Wilkinson, C. (2008) *Status of Coral Reefs of the World: 2008*. Global Coral Reef Monitoring Network and Reef and Rainforest Research Center, Townsville, Australia, 296 pp.
- Williams, I.D., Walsh, W.J., Claisse, J.T., Tissot, B.N. & Stamoulis, K.A. (2009) Impacts of a Hawaiian marine protected area network on the abundance and fishery sustainability of the yellow tang, *Zebrasoma flavescens*. *Biological Conservation*, 142, 1066–1073.