

Competition by obligate and facultative mutualists for partners in a shrimp-goby association

Patrick J. Lyons

Received: 21 January 2013 / Accepted: 2 January 2014 / Published online: 10 January 2014
© Springer Science+Business Media Dordrecht 2014

Abstract Mutualist species compete intra and inter-specifically for the resources provided by their partners. Because obligate mutualists are more reliant than facultative mutualists on the resources that their partners provide, they are expected to compete more strongly for those resources. Here, I examined interference competition in two goby fishes: *Nes longus* (an obligate mutualist) and *Ctenogobius saepepallens* (a facultative mutualist). Both gobies associate with the shrimp, *Alpheus floridanus*. Shrimp provide gobies with refuge from predators (a burrow in the sand), and gobies provide shrimp with a warning signal when predators are near. Using an aquarium experiment, I examined the behavior of a pair of gobies with access to a single shrimp burrow. I used four different goby pairings: large *N. longus* and small *N. longus*, large *N. longus* and small *C. saepepallens*, large *C. saepepallens* and small *N. longus*, and large *C. saepepallens* and small *C. saepepallens*. When paired with large *N. longus* individuals, small gobies of both species were less likely to occupy the single burrow than when paired with large *C. saepepallens* individuals. In addition, large *N. longus*

individuals were less likely to co-occupy the single burrow with smaller gobies than were large *C. saepepallens* individuals. These results seem to indicate that large *N. longus* individuals exclude smaller gobies from burrows, while large *C. saepepallens* individuals do not. This study adds evidence to the supposition that obligate mutualists in general compete more strongly for mutualist partners than do facultative mutualists.

Keywords Mutualism · Competition · Shrimp-goby · Alpheid · Obligate · Facultative

Introduction

Mutualism has been defined in many ways, but it is generally agreed that mutualism is an interspecific association in which both interacting species receive a benefit (Boucher et al. 1982). Between pairs of interacting mutualist partners, resources are exchanged and the benefit of gaining a resource outweighs the cost of providing one (Schwartz and Hoeksema 1998). The provisioned resource is often of minimal cost to produce, but of great value to the recipient (Connor 1995). Mutualist species can be subdivided based on the level of dependency on their mutualist partner (Boucher et al. 1982). Obligate mutualists are those whose survival is contingent upon the mutualist partner and are consequently never found in the absence of the partner. In contrast, facultative mutualists gain a fitness advantage from their mutualist partner but their survival is not

P. J. Lyons (✉)
Department of Ecology and Evolution,
Stony Brook University,
Stony Brook, NY 11794, USA
e-mail: patrick.lyons5@gmail.com

Present Address:
P. J. Lyons
CIEE Research Station Bonaire,
Kaya Gobernador N. Debrot 26, Kralendijk, Bonaire,
Netherlands Antilles

reliant upon them. A lack of reliance may be the results of multiple options, i.e. the resource provided by their partner can be gained through other means. For example, in cleaning mutualism in which smaller “cleaners” remove parasites from larger “clients,” many cleaners are considered facultative because they consume parasites as well as non-parasitic food items (Côté 2000).

Competition is an important component that shapes the dynamics of mutualisms (Addicott 1985; Jones et al. 2012). Individuals within and between species are likely to compete for access to resources provided by the mutualist partner species with losers suffering a fitness consequence (Jones et al. 2012). For example, between various ant and aphid species, a mutualism exists in which aphids provide nectar (a food resource) and ants provide protection from predators (Stadler and Dixon 2005). Aphids compete for the protective services of ants through exploitative competition. An increase in the density of aphids (greater competition for ant partners) has been shown to have negative fitness consequences for aphids in the form of higher predation rates (Cushman and Addicott 1989; Cushman and Whitham 1991). Different aphid species have differing competitive abilities (attractiveness to ants) based on the quality of their nectar. Those with lower quality nectar are less attractive to ants and of lower competitive ability. Such aphids that produce low quality nectar are visited by ants less frequently and consequently attacked by predators more often (Fischer et al. 2001).

Competition is an important component of cleaning mutualism as well. For cleaners, the resource gained is food in the form of the parasites attached to cleaners. When there are multiple cleaners in close proximity, more mobile clients can “choose” which cleaner to interact with and go to those that provide the best cleaning service (Bshary and Schäffer 2002). In this situation, cleaners compete for access to clients, and have been shown to provide better cleaning service than when clients do not have a “choice” between multiple cleaners (Adam 2010). Thus, the strength of competition has a large effect on the dynamics of the interaction between mutualist partners.

Given that obligate mutualists are more reliant on the resources provided by their mutualist partners than are facultative mutualists (Fiala et al. 1994; Heil et al. 2001; Stadler et al. 2002; Lyons 2013), we should expect that obligate mutualists should compete for those resources more strongly than facultative mutualists. When mutualists engage in exploitative competition, obligate

mutualists are likely to provide higher quality resources to their partners than are facultative mutualists. By providing a higher quality resource, a mutualist will be of greater attractiveness to the mutualist partner and more likely to gain the resource provided by that partner. For example, plant species that are dependent on insects for pollination (obligate mutualists) provide higher quality pollen than plant species that are facultative mutualists, i.e. pollinated by wind and insects (Hanley et al. 2008). Consequently, obligate insect-pollinated plants are visited by insects more often than are wind/insect-pollinated plants (Hanley et al. 2008).

When mutualist species engage in interference competition in addition to exploitative competition, obligate mutualists are expected to be stronger competitors than facultative mutualists. This is found between two damselfish species that inhabit and compete for the same anemone species, *Heteractis magnifica* (Holbrook and Schmitt 2002, 2004). *Amphiprion chrysopterus*, which is more reliant on *H. magnifica*, i.e., lives within anemones from recruitment until death, is competitively superior to *D. trimaculatus*, which inhabits anemones only during its juvenile phase (Schmitt and Holbrook 2003).

In the present study, I examined interference competition between an obligate and facultative species that compete for the same partner species. I focus on the mutualism that occurs between some species of alpheid shrimp and gobiid fishes (Longley and Hildebrand 1941; Karplus 1987; Karplus and Thompson 2011). One or two shrimp construct a burrow that is cohabited with one or two goby partners. These shrimp have poor vision and are prone to predation while outside the burrow foraging or maintaining the burrow entrance (Jaafar and Zeng 2012). However, shrimp use certain behaviors of gobies as indication that danger is present, thus allowing shrimp to emerge only when it is safe to do so. From this association, gobies gain a shelter from predators. Competition for shrimp partners is likely an important component of shrimp-goby mutualism. For example, by artificially inflating the density of the goby *Ctenogobius feroculus* in an area, Thompson (2005) demonstrated that larger gobies ejected smaller gobies from their burrows. Those ejected gobies were presumed to be consumed for lack of a shrimp partner.

In the Western Atlantic, the shrimp *Alpheus floridanus* associates with several species of gobies including *Nes longus*, *Ctenogobius saepepallens*, *Bathygobius curacao*, and *Oxyurichthys stigmalocephalus* (Longley and Hildebrand 1941; Wayman 1973; Weiler

1976; Karplus 1992; Randall et al. 2005; Kramer et al. 2009; Lyons 2012; Lyons 2013). Only one species (*N. longus*) has been described as an obligate mutualist (Karplus 1992; Randall et al. 2005; Lyons 2013). The rest are considered facultative mutualists.

I previously found that *N. longus* and *C. saepepallens* use burrows of *A. floridanus* very differently (Lyons 2013). *Ctenogobius saepepallens* meanders between burrows, while *N. longus* remains at individual burrows on average 2.52 ± 1.41 days (Mean \pm 95 % CI; Lyons 2012). Differences in how the two gobies use burrows is likely related to how they respond to competitors for burrows. Karplus (1992) and Randall et al. (2005) reported from observations in Miami, Florida and Glover's Reef, Belize, respectively that *N. longus*, but not *C. saepepallens*, prevents other gobies from using burrows by chasing and nipping them. In contrast, Kramer et al. (2009) reported no observations of these behaviors of either goby species in Curacao, Netherlands Antilles. Preliminary observations at the location of the present study in the Bahamas revealed that *N. longus* may aggressively prevent other gobies from remaining in the periphery of the burrows of their host shrimps. My first hypothesis is that large *N. longus* individuals prevent smaller gobies from remaining at shrimp burrows, but large *C. saepepallens* individuals do not.

Randall et al. (2005) reported that roaming *C. saepepallens* individuals will dive into the nearest burrow when frightened, even when that burrow is occupied by another goby. I have made similar observations in the location of the present study. These observations would seem to indicate that even if small gobies are prevented from remaining near or inside shrimp burrows, they still might be able to use shrimp burrows for protection from predators. Thus, my second hypothesis is that excluded goby individuals will dive into occupied burrows when frightened.

Methods

All experiments were carried out at the Perry Institute for Marine Sciences, Lee Stocking Island, Bahamas. I included *Nes longus*, *Ctenogobius saepepallens*, and *Alpheus floridanus* in the study. Gobies and shrimp were collected near Normans Pond Cay (23°45'35.64"N, 76°7'59.64"W) with the use of SCUBA. I captured gobies using aquarium nets and captured shrimp using the trapping method described by Karplus and Vercheson

(1978). Gobies and shrimp were maintained in 190-l aquaria that were part of a flow-through seawater system. Both gobies and shrimp were fed ad libitum.

Experiments were conducted in 190-l aquaria with sand on the bottom 10 cm deep. Artificial shrimp burrows were made of PVC tubing 20 cm long with a 2.5 cm inner diameter. The use of artificial burrows has been well established in studies of shrimp-goby associations (Karplus et al. 1972; Zeng and Jaafar 2012; Hou et al. 2013). These tubes were dug into the sand at a 40° angle such that one end protruded from the sand. I filled the bottom half of each tube with sand. These artificial burrows were suitable surrogates for natural *A. floridanus* burrows for two reasons. First, they were similar in diameter to natural burrows (Dworschak and Ott 1993). Second, both goby species and *A. floridanus* assumed normal behaviors in artificial burrows. For example, *A. floridanus* excavated sand from within artificial burrows and *N. longus* guarded resident shrimp with caudal fin warnings. In previous experiments, I have found that gobies of both species and of various sizes are attracted to these burrows (Lyons 2012).

Before experiments, a single artificial burrow was placed in the middle of a 190-l aquarium. A shrimp was placed in the aquarium and allowed to acclimate for at least 1 h after entering the burrow. Two gobies were placed in the aquarium, and after 1 h, I recorded whether each goby was inside or outside the burrow (hypothesis one). The cut-off time for each trial was 1 h. No trials resulted in neither goby in the burrow, but some trials resulted in both gobies co-occupying the burrow. If one goby was still outside the burrow, I moved an aquarium net across the length of the aquarium to frighten the focal goby (Rodewald and Foster 1998; Bergstrom 2002) and recorded whether it retreated into the burrow or remained on bare sand (hypothesis two).

I carried out four trial types with different goby-size combinations: (A) one large and one small *N. longus*, (B) one large and one small *C. saepepallens*, (C) one large *N. longus* and one small *C. saepepallens*, and (D) one large *C. saepepallens* and one small *N. longus*. In each trial, the larger goby was ≥ 1 cm longer (total length) than the smaller goby. No individual goby was included in more than one trial. 20 trials were conducted for each goby-size combination.

I used eight total G-tests of independence to determine (A) if the smaller goby occupied the burrow more often than the larger goby in each of the four trial types

(four separate G-tests), (B) if smaller gobies were more likely to occupy burrows with larger *N. longus* or larger *C. saepepallens* (one G-test), (C) if larger *N. longus* or larger *C. saepepallens* were more likely to co-occupy burrows with the smaller gobies (one G-test) and (D) if smaller gobies were more likely to occupy than retreat to burrows when paired with a larger *N. longus* and larger *C. saepepallens* (two separate G-tests).

To compensate for the inflated type-one error rate associated with multiple testing, I applied Bonferroni (Sokal and Rohlf 1994), Holm (1979), Hochberg (1988), and Hommel (1988) corrections to the P-values. All of these corrections yielded similar results and did not change the statistical significance of any of the results. Thus, I report P-values with a Bonferroni correction.

Results

In trials including large *Nes longus*, the burrow was occupied by the larger *N. longus* individual more often than the smaller *N. longus* ($G_{adj}=14.73$, $df=1$, $P<0.001$, Fig. 1) or smaller *Ctenogobius saepepallens* individual ($G_{adj}=27.15$, $df=1$, $P<0.001$, Fig. 1). In trials including large *C. saepepallens*, the burrow was occupied as often by the larger *C. saepepallens* individual as the smaller *N. longus* ($G_{adj}=2.05$, $df=1$, $P=1.0$, Fig. 1) or smaller *C. saepepallens* individual ($G_{adj}=2.16$, $df=1$, $P=1.0$, Fig. 1). Smaller gobies occupied burrows more often when paired with a larger *C. saepepallens* individuals than larger *N. longus*

individuals (26/40 times and 7/40 times, respectively; $G_{adj}=16.18$, $df=1$, $P<0.001$; Fig. 1).

Large *C. saepepallens* individuals co-occupied burrows with smaller individuals more often than larger *N. longus* individuals (12 of 25 times occupied versus 4 of 37 times occupied; $G_{adj}=9.54$, $df=1$, $P=0.016$; Fig. 1).

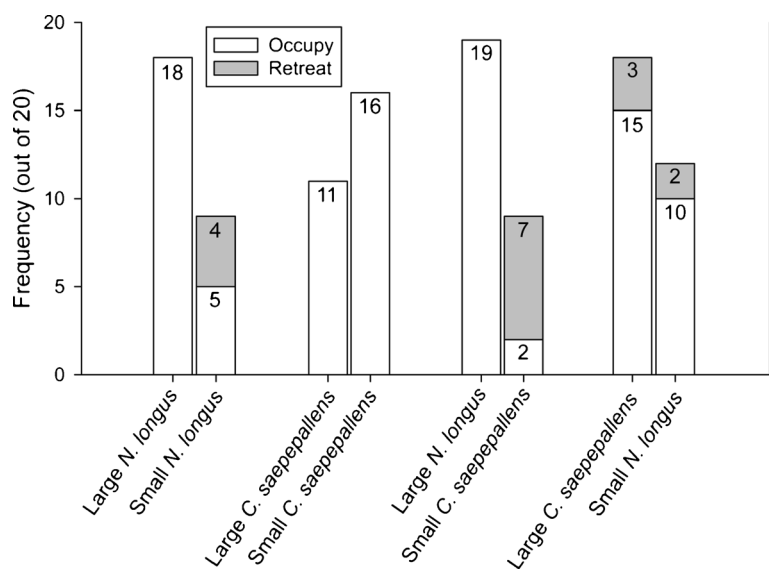
When paired with large *N. longus* individuals, smaller gobies occupied burrows as often as they retreated from the aquarium net into burrows (7/40 times versus 11/40 times, respectively; $G_{adj}=1.037$, $df=1$, $P=1.0$; Fig. 1). When paired with larger *C. saepepallens*, smaller gobies occupied burrows more often than they retreated from the aquarium net into burrows (26/40 versus 2/40 times, respectively; $G_{adj}=30.54$, $df=1$, $P<0.001$; Fig. 1).

Discussion

I provide evidence that large *Nes longus* individuals exclude smaller gobies from burrows, irrespective of the species of the smaller goby. In contrast, large *Ctenogobius saepepallens* individuals do not seem to exclude smaller gobies from burrows. The results also provide evidence that even when large competitively dominant *N. longus* prevent smaller gobies from remaining in burrows, those smaller gobies can still retreat into burrows while avoiding predators.

In many shrimp-goby associations, larger gobies tend to associate with larger shrimp and smaller gobies with smaller shrimp (Jaafar and Hou 2012). Evidence suggests

Fig. 1 Outcomes of goby competition trials. Paired bars are from the same trial combination type, ex. Large *N. longus*—Small *N. longus*, Large *C. saepepallens*—Small *C. saepepallens*, etc. There were 20 replicate trials for each combination type. Numbers within bars denote times a goby occupied a burrow after 1 h (empty bars) or retreated into a burrow if outside the burrow (grey bars). Burrows were occupied by both gobies (co-occupied) 3, 7, 1, and 5 times in the four trial combinations going from left to right



that size sorting is mediated by intraspecific competition. In a recent paper on the association between the goby *Myersina macrostoma* and shrimp *Alpheus rapax*, Jaafar and Hou (2012) demonstrated that *M. macrostoma* visually select and prefer larger *A. rapax* burrows to smaller *A. rapax* burrows or other shelter (rocks). Larger shrimp build larger burrows than smaller shrimp. Jaafar and Hou (2012) suggest that size sorting is due to competitive dominance by larger gobies that prefer larger burrows. Further evidence that size sorting is mediated by intraspecific competition has been found in the association between the goby *Ctenogobius feroculus* and shrimp *Alpheus djeddensis*. Thompson (2005) demonstrated that small *C. feroculus* only associate with large *A. djeddensis* when large *C. feroculus* are absent. Large *C. feroculus* were never found to associate with small *A. djeddensis* possibly because of size constraints of small burrows (Thompson 2005). Size sorting is found in the association between *N. longus* and *Alpheus floridanus*, but not between *C. saepepallens* and *A. floridanus* (Randall et al. 2005). This makes sense given my finding here that large *N. longus* excludes smaller gobies from burrows, but large *C. saepepallens* do not.

My past work suggests two non-exclusive explanations why large *N. longus* exclude smaller gobies while large *C. saepepallens* do not. First, *N. longus* is more dependent on shrimp burrows for shelter than is *C. saepepallens*. *Nes longus* avoids predators more effectively while using shrimp burrows than conch shells for refuge (Lyons 2013). In contrast, *C. saepepallens* avoids predators with equal effectiveness while using shrimp burrows or conch shells as refuge (Lyons 2013). Thus, *N. longus* has greater fitness gains than *C. saepepallens* while using available *A. floridanus* burrows. These large fitness gains could promote greater aggression and exclusion of smaller gobies.

Second, *N. longus* is more dependent on the immediate vicinity of burrow entrances for foraging than is *C. saepepallens*. Both *N. longus* and *C. saepepallens* feed on infaunal invertebrates such as crustaceans, gastropods, molluscs, and nematodes (Wayman 1973; Randall et al. 2005; Lyons 2012). *Nes longus* is a visual sit-and-wait predator that does not venture far from burrow entrances and feeds exclusively in the periphery of burrow entrances (Kramer et al. 2009; Lyons 2012). In contrast, *C. saepepallens* forages over a broader area by winnowing, i.e. engulfing scoops of sand and sorting desired from undesired particles on the gill rakers (Langeland and Nøst 1995; McCormick

1998). Because *N. longus* restricts its foraging range to the periphery of burrow entrances, it likely has greater incentive than *C. saepepallens* for aggressive exclusion of other gobies from its restricted foraging range.

There are of course other possible explanations that could account for the differences in territorial aggression between large *N. longus* and large *C. saepepallens* individuals. For example, differences in reproductive strategy (type of larvae, location of eggs, etc.) could be important. However, information that could validate or invalidate this explanation and others not mentioned is lacking. Because differences in competitive strength probably shape mutualism networks (Jaafar and Hou 2012) and have important effects on population dynamics of the species involved (Holbrook and Schmitt 2004), it is important that further research examines the different reasons why obligate mutualists may compete more strongly than facultative mutualists.

Acknowledgments Helpful comments on the manuscript were provided by A. Thompson, my PhD advisor, J. Levinton, and three anonymous reviewers. Field and laboratory assistance was provided by I. Chambers and C. Kiel. Technical assistance was provided by I. Black and E. Lamarre. Materials were provided by C. Thacker. This research was supported by the W. M. Keck Foundation Program in Molecular Systematics and Evolution at the Natural History Museum of Los Angeles County and a Sigma Xi Grant in Aid of Research. This project was conducted with IACUC approval # 2010-1837 and in compliance with the Ministry of Agriculture and Marine Resources, Bahamas.

References

- Adam TC (2010) Competition encourages cooperation: client fish receive higher-quality service when cleaner fish compete. *Anim Behav* 79(6):1183–1189
- Addicott JF (1985) Competition in mutualistic systems. In: Boucher DH (ed) *The biology of mutualism: ecology and evolution*. Oxford University Press, New York, pp 217–247
- Bergstrom C (2002) Fast-start swimming performance and reduction in lateral plate number in threespine stickleback. *Can J Zool* 80(2):207–213
- Boucher DH, James S, Keeler KH (1982) The ecology of mutualism. *Annu Rev Ecol Syst* 13:315–347
- Bshary R, Schäffer D (2002) Choosy reef fish select cleaner fish that provide high-quality service. *Anim Behav* 63(3):557–564
- Connor RC (1995) The benefits of mutualism: a conceptual framework. *Biol Rev* 70(3):427–457
- Côté I (2000) Evolution and ecology of cleaning symbioses in the sea. *Oceanogr Mar Biol Annu Rev* 38:311–355
- Cushman LH, Addicott JF (1989) Intra- and interspecific competition for mutualists: ants as a limited and limiting resource for aphids. *Oecologia* 79(3):315–321

- Cushman JH, Whitham TG (1991) Competition mediating the outcome of a mutualism: protective services of ants as a limiting resource for membracids. *Am Nat* 138(4):851–865
- Dworschak PC, Ott JA (1993) Decapod burrows in mangrove-channel and back-reef environments at the Atlantic Barrier Reef, Belize. *Ichnos* 2:277–290
- Fiala B, Grunsky H, Maschwitz U, Linsenmair KE (1994) Diversity of ant-plant interactions: protective efficacy in *Macaranga* species with different degrees of ant association. *Oecologia* 97(2):186–192
- Fischer MK, Hoffmann KH, Völkl W (2001) Competition for mutualists in an ant-homopteran interaction mediated by hierarchies of ant attendance. *Oikos* 92(3):531–541
- Hanley ME, Franco M, Pichon S, Darvill B, Goulson D (2008) Breeding system, pollinator choice and variation in pollen quality in British herbaceous plants. *Funct Ecol* 22(4):592–598
- Heil M, Fiala B, Maschwitz U, Linsenmair KE (2001) On benefits of indirect defence: short- and long-term studies of antiherbivore protection via mutualistic ants. *Oecologia* 126(3):395–403
- Hochberg Y (1988) A sharper Bonferroni procedure for multiple tests of significance. *Biometrika* 75(4):800–802
- Holbrook SJ, Schmitt RJ (2002) Competition for shelter space causes density-dependent predation mortality in damselfishes. *Ecology* 83(10):2855–2868
- Holbrook SJ, Schmitt RJ (2004) Population dynamics of a damselfish: effects of a competitor that also is an indirect mutualist. *Ecology* 85(4):979–985
- Holm S (1979) A simple sequentially rejective multiple test procedure. *Scand J Stat* 6:65–70
- Hommel G (1988) A stagewise rejective multiple test procedure based on a modified Bonferroni test. *Biometrika* 75(2):383–386
- Hou Z, Liew J, Jaafar Z (2013) Cleaning symbiosis in an obligate goby–shrimp association. *Mar Biol*. doi:10.1007/s00227-013-2252-2
- Jaafar Z, Hou Z (2012) Partner choice in Gobiid fish *Myersina macrostoma* living in association with the alpheid shrimp *Alpheus rapax*. *Symbiosis* 56(3):121–127
- Jaafar Z, Zeng Y (2012) Visual acuity of the goby-associated shrimp, *Alpheus rapax* Fabricius, 1798 (Decapoda, Alpheidae). *Crustaceana* 85(12–13):1487–1497
- Jones EI, Bronstein JL, Ferrière R (2012) The fundamental role of competition in the ecology and evolution of mutualisms. *Ann N Y Acad Sci* 1256(1):66–88
- Karplus I (1987) The association between gobiid fishes and burrowing alpheid shrimps. *Oceanogr Mar Biol Annu Rev* 25:507–562
- Karplus I (1992) Obligatory and facultative goby–shrimp partnerships in the western tropical Atlantic. *Symbiosis* 12(3):275–291
- Karplus I, Thompson AR (2011) The partnership between gobiid fishes and burrowing alpheid shrimp. In: Patzner RA, Van Tassell JL, Kovacic M, Kapoor BG (eds) *Biology of gobies*. Science Publishers, Inc., New Hampshire, pp 559–608
- Karplus I, Vercheson A (1978) A method for collecting live alpheid shrimp and their symbiotic gobiid fish partners. *Crustaceana* 34(2):220–222
- Karplus I, Tsumamal M, Szlep R (1972) Analysis of the mutual attraction in the association of the fish *Cryptocentrus cryptocentrus* (Gobiidae) and the shrimp *Alpheus djiboutensis* (Alpheidae). *Mar Biol (Berl)* 17(4):275–283
- Kramer A, Van Tassell JL, Patzner RA (2009) A comparative study of two goby shrimp associations in the Caribbean Sea. *Symbiosis* 49(3):137–141
- Langeland A, Nøst T (1995) Gill raker structure and selective predation on zooplankton by particulate feeding fish. *J Fish Biol* 47(4):719–732
- Longley W, Hildebrand S (1941) Systematic catalog of the fishes of Tortugas, Florida. Carnegie Institute of Washington Publication 353, 331 pp
- Lyons PJ (2012) The evolution of mutualism between alpheid shrimp and gobiid fishes: a balance between benefits and costs. Dissertation, Stony Brook University
- Lyons PJ (2013) The benefit of obligate versus facultative strategies in a shrimp–goby mutualism. *Behav Ecol Sociobiol* 67(5):737–745
- McCormick M (1998) Ontogeny of diet shifts by a microcarnivorous fish, *Cheilodactylus spectabilis*: relationship between feeding mechanics, microhabitat selection and growth. *Mar Biol* 132(1):9–20
- Randall JE, Lobel PS, Kennedy CW (2005) Comparative ecology of the gobies *Nes longus* and *Ctenogobius saepepallens*, both symbiotic with the snapping shrimp *Alpheus floridanus*. *Environ Biol Fish* 74(2):119–127
- Rodewald AD, Foster SA (1998) Effects of gravidity on habitat use and antipredator behaviour in three-spined sticklebacks. *J Fish Biol* 52(5):973–984
- Schmitt RJ, Holbrook SJ (2003) Mutualism can mediate competition and promote coexistence. *Ecol Lett* 6(10):898–902
- Schwartz MW, Hoeksema JD (1998) Specialization and resource trade: biological markets as a model of mutualisms. *Ecology* 79(3):1029–1038
- Sokal R, Rohlf J (1994) *Biometry: the principles and practices of statistics in biological research*. W. H Freeman, New York
- Stadler B, Dixon AFG (2005) Ecology and evolution of aphid–ant interactions. *Annu Rev Ecol Evol Syst* 36:345–372
- Stadler B, Dixon AFG, Kindlmann P (2002) Relative fitness of aphids: effects of plant quality and ants. *Ecol Lett* 5(2):216–222
- Thompson AR (2005) Dynamics of demographically open mutualists: immigration, intraspecific competition, and predation impact goby populations. *Oecologia* 143(1):61–69
- Wayman CW (1973) Comparative ecology of three sympatric species of gobies from Belize (British Honduras), *Nes longus* (Nichols), *Gobionellus saepepallens* Gilbert and Randall and *Coryphopterus glaucofraenum* Gill. Thesis, Northern Illinois University
- Weiler DA (1976) Burrow-dwelling fishes in a back-reef area and their relation to sediment grain size. Thesis, University of Puerto Rico
- Zeng Y, Jaafar Z (2012) Repetitive-motion display: a new behaviour in a burrowing alpheid shrimp. *J Crustac Biol* 32(5):693–697