Gobies on Coral Reefs

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INTRODUCTION

The family Gobiidae comprises at least 2000 species (Nelson, 2006), with many still undiscovered or undescribed. More than half of all goby species are found on coral reefs and thus they contribute greatly to the astonishing fish diversity of this environment. Most coral reef gobies are closely associated with the substratum, where they seek shelter from predators in the complex physical structure of reef habitat (Munday and Jones, 1998). As a consequence of their small size and cryptic life-style, careful investigations by trained experts are necessary to reveal their full diversity. Although there are few such researchers, new species are still being described (e.g., *Coryphopterus* (Victor, 2007), *Eviota* (Gill and Jewett, 2004),

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Gobiodon (Harold and Winterbottom, 1995; Harold and Winterbottom, 1999; Winterbottom and Harold, 2005), *Priolepis* (Nogawa and Endo, 2007) and *Trimma* (e.g. Winterbottom, 2004, 2006; Hagiwara and Winterbottom, 2007; Suzuki and Senou, 2007; Winterbottom and Zur, 2007). Despite the diversity of coral reef gobies – the genus *Trimma*, for example, may include nearly 100 species (Winterbottom and Southcott, 2008) – most species are easily overlooked and are commonly excluded from sampling or ecological surveys. However, a recent upsurge of interest in the ecological role of small reef fishes (e.g., Munday and Jones, 1998; Depczynski and Bellwood, 2003) and the use of several coral-reef goby genera as model groups in ecology and evolution (e.g., Forrester and Steele, 2000; Munday *et al.*, 2001; Taylor and Hellberg, 2003; Munday, 2004b) has greatly increased our understanding of the biology and ecology of this diverse and interesting group of coral reef fishes.

Gobies are not only diverse in terms of species richness, but also with regard to their life-styles and life-histories. Gobies occupy all major habitats around coral reefs, including sand and rubble, seagrass meadows, coral reef matrix, live corals and numerous other living organisms (Greenfield and Johnson, 1999; Nakamura and Sano, 2004; Syms and Jones, 2004). Size diminution has played an important role in the evolution of coral reef gobies and has enabled them to utilize many restricted or specialized microhabitats (Munday and Jones, 1998; Herler, 2007). The most habitat-specialized gobies are associated with invertebrates such as sponges, soft coral and hard coral (Larson, 1985, 1990; Munday *et al.*, 1997; Herler and Hilgers, 2005). Others do not use invertebrates as habitat, but use the structures created by them, such as the burrows of shrimps. Mutualistic relationships between shrimps and gobies are found in about 15 genera and most are obligate associates of burrowing alpheids.

Coral reef gobies hold two world records: the smallest size and the shortest lifespan among marine vertebrates (Winterbottom, 1990; Depczynski and Bellwood, 2005; Winterbottom and Southcott, 2008). Most reef gobies are short-lived species. Many are annuals (Kritzer, 2002; Hernaman and Munday, 2005a) and some have generation times of just a few months (Depczynski and Bellwood, 2005; Depczynski *et al.*, 2007; Winterbottom and Southcott, 2008). They are also among the most abundant families of fishes on coral reefs (Ackerman and Bellwood, 2000). High abundance combined with short lifespans means that they account for a very large proportion of the total growth production of reef fishes (Depczynski *et al.*, 2007). Consequently, these tiny reef fish contribute significantly to energy transfer throughout coral reef systems. Minute body size and short

lifespan are also associated with a range of morphological adaptations and reductions in the skeleton, fins, squamation and lateral line system in the smallest species (Winterbottom, 1990; Herler, 2007; Winterbottom and Zur, 2007).

High predation risk and a short lifespan are associated with early maturation in many small coral reef gobies. Early maturation is advantageous because it results in a higher probability of survival to first reproduction and shorter generation times (Stearns, 1992). A disadvantage is that maturation at a small body size limits batch fecundity and, potentially, spawning opportunities (i.e., in social systems where larger size confers greater success in competition for mates or spawning sites). Perhaps as a result of these limitations, many coral reef gobies invest in somatic growth throughout life including during reproduction (Hernaman and Munday, 2005a), which contrasts with many small, long-lived coral reef fishes where growth ceases soon after sexual maturation (e.g., Choat and Robertson, 2002).

Coral reef gobies also exhibit a diversity of reproductive behaviours and patterns of social organisation. Most, if not all, coral reef gobies are substrate spawners with parental egg care, but mating strategies vary from monogamy to polygyny (e.g., Kuwamura *et al.*, 1993; Sunobe and Nakazono, 1999a, 1999b; Takegaki and Nakazono, 1999; Hernaman and Munday, 2005b). Some species form complex social hierarchies where individuals queue for breeding rights, and growth rates are controlled by social interactions (Wong *et al.*, 2007; Wong *et al.*, 2008a; Wong *et al.*, 2008b). Many species also exhibit remarkable sexual flexibility and are able to change sex, in some cases more than once (Nakashima *et al.*, 1996; Munday *et al.*, 1998; Manabe *et al.*, 2007a).

In this chapter we examine the ecology, life-histories and reproductive behaviour of coral reef gobies. We also explore morphological adaptations that are associated with the unique life-styles exhibited by many coral reef gobies, and the extreme miniaturization of certain groups of species. Although frequently overlooked in studies of reef fish assemblages due to their small size and cryptic behaviour, we show that gobies play an important role in coral reef ecosystems, and that they have proven to be a useful model group for studying a broad range of topics in ecology and evolution, including: species diversification, ecological and morphological adaptation, the evolution of animal life history traits, mechanisms of community structure and population regulation, and the evolution of animal behaviour.

ECOLOGY

Habitat Associations

Gobies inhabit most microhabitats associated with coral reefs (Fig. 4.2.1), and at the same time are among the most habitat-specialized reef fish groups. This apparent contradiction occurs because at the family level, gobies occupy nearly every habitat type present on coral reefs, yet many species are habitat-specialist with precise microhabitat requirements (Munday *et al.*, 1997; Greenfield and Johnson, 1999; Depczynski and Bellwood, 2004; Herler, 2007). Most coral reef gobies are epibenthic or cryptobenthic (Miller, 1996); there are very few nektonic species. Coral reefs are physically complex structures that offer many options for cryptobenthic life-styles (Fig. 4.2.2). The small body size of gobies enables them to exploit habitats and food resources that are not available to larger species. The opportunity to utilize a wide range of microhabitats at small spatial scales appears to have contributed to the extraordinary diversity of species within some genera, such as *Trimma, Eviota* and *Gobiodon* (Munday and Jones, 1998; Munday *et al.*, 2004).

The most habitat-specialized gobies are found in obligate association with living hosts, including sponges (Larson, 1990; Rocha *et al.*, 2000; Colin, 2002; Taylor and Hellberg, 2005), hydrozoans (Larson, 1985; Herler and Hilgers, 2005), octocorals (Larson, 1985, 1990), scleractinian corals (Larson, 1985; Munday *et al.*, 1997; Herler, 2007), antipatharians (Munday *et al.*, 2002; Herler, 2007), ascidians (Larson, 1990) and even plants, such as seagrasses (Larson, 1990). The best studied of these habitat specialists are the coral-dwelling gobies from the genus *Gobiodon*, which live among the branches of scleractinian corals from the family Acroporidae. These coral-dwelling gobies have been used as a model group for understanding the evolution and ecology of habitat specialization (e.g. Munday *et al.*, 1997, 2001; Munday *et al.*, 2004), and the consequences of habitat specialization in the face of increasing anthropogenic stresses to coral reefs (Munday, 2004b; Feary, 2007; Schiemer *et al.*, 2009). Although all species of coral-dwelling gobies can be considered habitat-specialists in the broad sense, there is a vast difference in the degree of specialization among species. Some species of *Gobiodon* are associated with just a single coral species throughout their entire geographic range (Munday, 2002; Munday *et al.*, 2004), whereas other species inhabit up to 10 - 20 different species of coral and change preferences among locations depending on the availability of different coral species (Munday *et al.*, 1997; Munday, 2002; Dirnwöber and Herler, 2007).
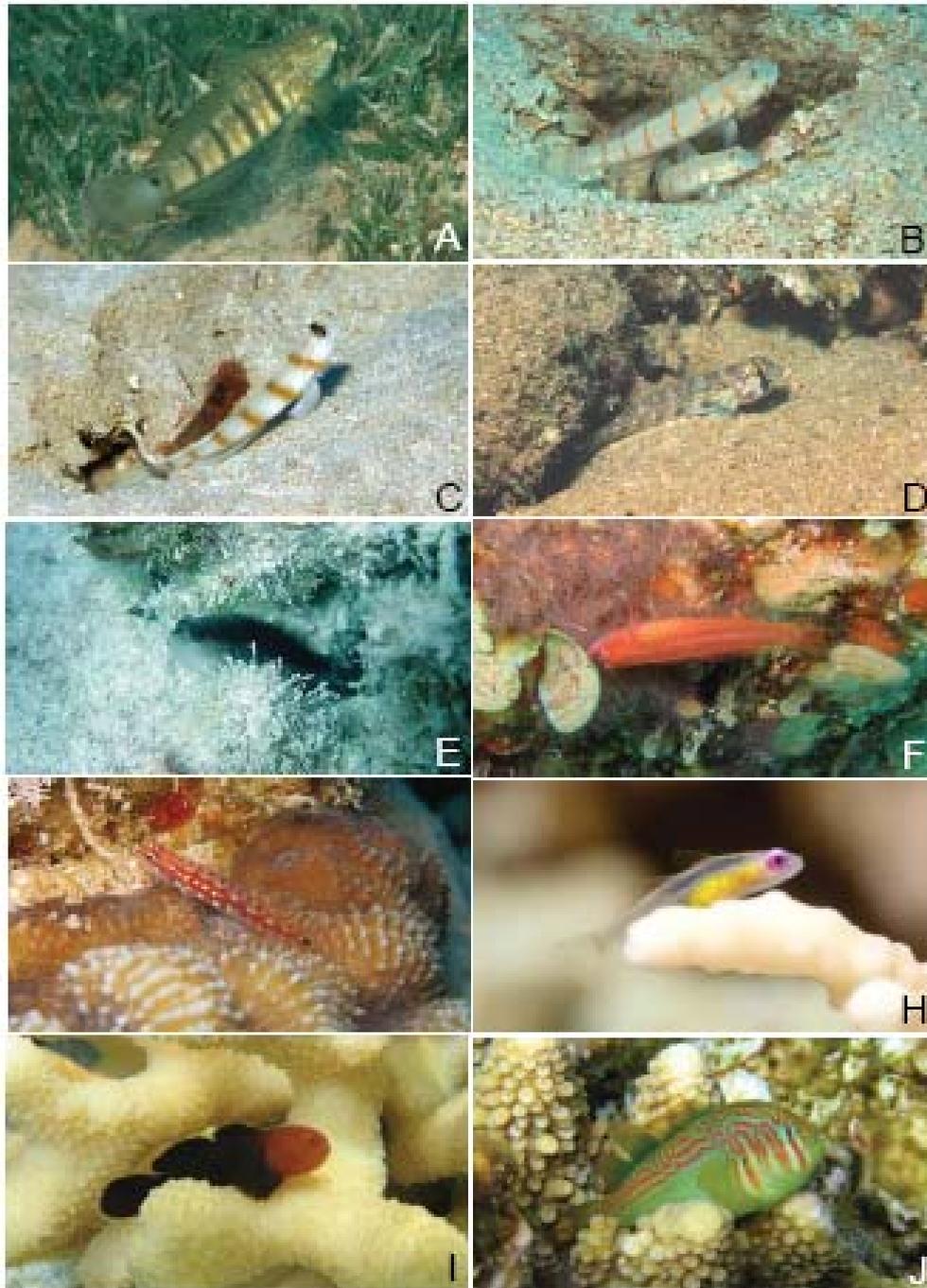
Fig. 4.2.1 Ten Indo-Pacific gobiid species as examples of the various life-styles of coral reefs gobies. A: *Amblygobius albimaculatus* sifting sand in a seagrass meadow. B: a pair of *Valenciennea puellaris* at the entrance of their self-dug burrow. C: *Amblyeleotris sungami* which lives in a mutualistic relationship with a species of *Alpheus* snapping shrimp. D: *Gnatholepis anjerensis* on the edge between coral rock and sand bottom. E: *Asterropteryx semipunctata* between algae on coral rubble. F: *Trimma avidori* swimming upside down in a small coral rock cave. G: *Eviota zebrina* inhabits live corals and coral rock. H: *Bryaninops natans* is an obligate associate of *Acropora* corals. I: *Paragobiodon echinocephalus* in the pocilloporid coral *Stylophora pistillata*. J: *Gobiodon histrio* among branches of *Acropora gemmifera*. Photographs by J. Herler.
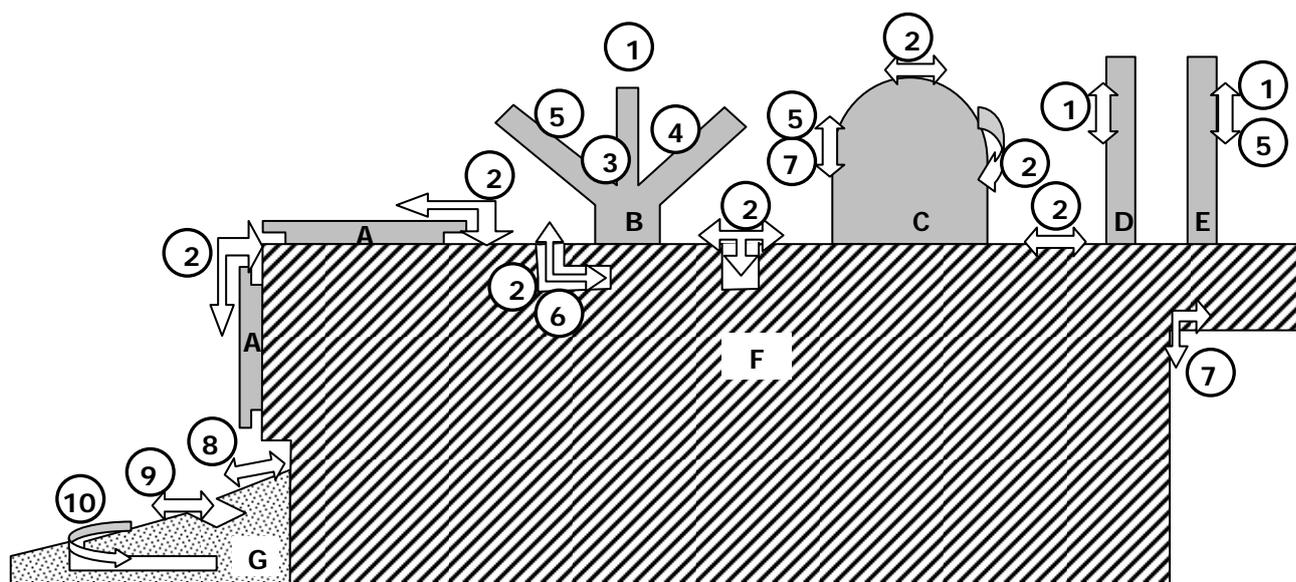
Fig. 4.2.2 Schematic presentation of coral, coral-rock and soft-sediment microhabitats used by coral reef gobies (modified from Herler, 2007). Grey structures represent living coral colonies, cross-hatched areas represent coral rock and stippled areas represent sand. Arrows indicate major movement and escape directions. Microhabitats are indicated by letters: A-C: different growth forms of scleractinian corals; A: plate-like and encrusting corals, B: branching corals (*Acropora* spp., *Stylophora pistillata*), C: massive corals; D: hydrozoan coral *Millepora dichotoma*; E: antipatharian and soft corals; F: coral rock; G: sand. Representative examples of gobiid genera are indicated by numbers: 1: *Bryaninops* spp., 2: *Eviota* spp.; 3: *Gobiodon* spp.; 4: *Paragobiodon* spp.; 5: *Pleurosicya* spp.; 6: *Priolepis* spp.; 7: *Trimma* spp.; 8: *Asterropteryx* spp., *Coryphopterus* spp., *Fusigobius* spp., *Gnatholepis* spp., *Istigobius* spp.; 9: *Amblygobius* spp., *Valenciennea* spp.; 10: *Amblyeleotris* spp., *Cryptocentrus* spp., *Ctenogobiops* spp., *Vanderhorstia* spp..

The intimate association of some gobies with coral habitat has implications for their distributions and abundances. Coral hosts appear to be a limiting resource for some species of *Gobiodon*, and consequently their abundances within and among reefs are often closely correlated with the abundance of their preferred coral species (Kuwamura *et al.*, 1994; Munday *et al.*, 1997; Munday, 2000). Furthermore, coral loss from bleaching or other disturbances usually causes dramatic declines in the abundances of coral-dwelling gobies (Munday *et al.*, 1997; Munday, 2004b; Feary *et al.*, 2007). The specialist species that inhabit just one or two species of coral usually fare worse when coral cover declines than do the generalist species (Munday, 2004b). The reason for this appears to be that the highly specialist species are unable to use alternative corals when the abundance of their preferred hosts decline, whereas the more generalist species shift to a range of alternative coral hosts even when their preferred habitats become less abundant.

Habitat specialization and the capacity to use alternative hosts is linked to the ecological performance of gobies within their habitat. Caley and Munday (2003) demonstrated that there was a trade-off between habitat specialization and growth rate among *Gobiodon* species. Two specialist species, *G. histrio* and *G. brochus,* grew much faster on their preferred host coral compared to a less preferred coral species. In contrast, the growth of two generalist species, *G. quinquestrigatus* and *G. oculolineatus,* differed little between the two coral species. Importantly, the growth of the specialists on their preferred coral host was significantly higher than that of the generalists on the same coral host, demonstrating that habitat specialists have superior performance on the preferred habitats. This illustrates that habitat specialists out-perform habitat generalists on their preferred habitat, but they are unable to maintain their performance between habitats. In contrast, generalists perform equally well on most habitat types. This trade-off between habitat specialization and performance helps explain why both habitat-specialist and generalist species are able to persist in animal communities. Furthermore, it helps explain why specialist species decline rapidly when their preferred habitats decline in abundance (Fig. 4.2.3).
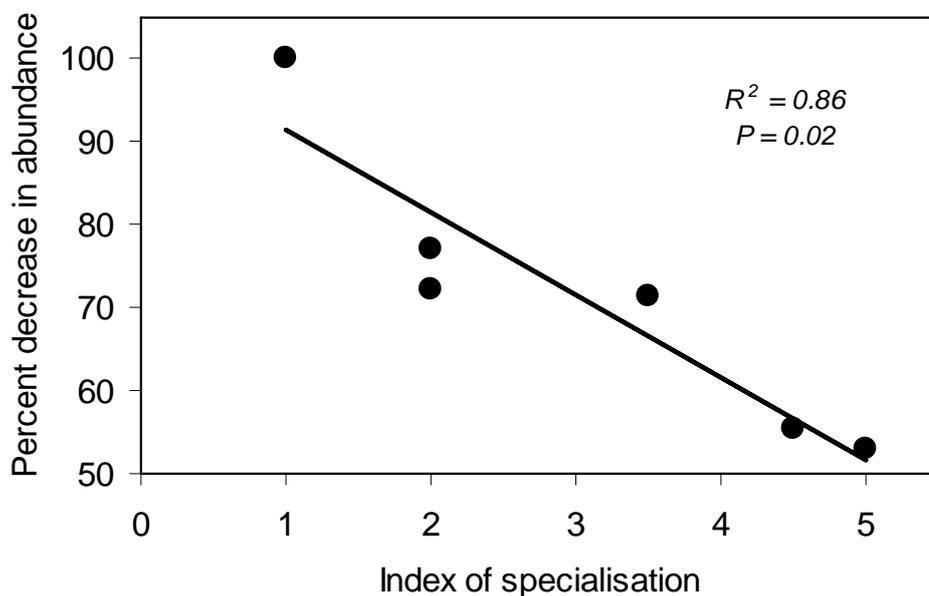

Fig. 4.2.3 Proportional decline in population size of six coral-dwelling goby species (genus *Gobiodon*) following severe loss of live coral habitat (modified from Munday, 2004b). Specialist species declined proportionally more than generalist species. The specialization index for each goby species was calculated by summing the total number of coral species that were used by each goby species either in proportion with availability (score of 0.5) or more frequently than expected from availability (score of 1.0). Habitat specialization data from Munday (2000).

Habitat specialization has also led to a range of other adaptive specializations in coral reef gobies. For example, coral-dwelling gobies exhibit remarkable capacity for hypoxia tolerance and air breathing (Nilsson *et al.*, 2004; Nilsson *et al.*, 2007). Oxygen levels among the branches of coral colonies can decline dramatically overnight due to the respiration of the coral host (Nilsson *et al.*, 2004). All species of coral-dwelling gobies are able to tolerate very low oxygen levels, presumably because such conditions are regularly encountered within their preferred habitats. Furthermore, species of *Gobiodon* associated with shallow-water corals that become air exposed during low tides have evolved a greater capacity for air-breathing than species associated with deeper-water corals that never become exposed to air (Nilsson *et al.*, 2007). Finally, the loss of scales that appears to be associated with the capacity for air-breathing across the skin (Nilsson *et al.*, 2007) is also associated with the presence of toxin glands in coral-dwelling gobies. In addition to their potential role in predator deterrence (Lassig, 1981; Schubert *et al.*, 2003), these toxins help protect the otherwise unprotected skin surface from attack by external parasites (Munday *et al.*, 2003). Therefore, it appears the specialized habitat associations of coral-dwelling gobies have led to the evolution of morphological adaptations to their coral habitat.

Many other coral reef gobies are much less specialized in their habitat choices than the coral-dwelling gobies discussed above, but nevertheless they still have habitat preferences. These preferences are seen in the distribution of species among reef environments (Greenfield and Johnson, 1999; Depczynski and Bellwood, 2004; Herler, 2007; Hernaman and Probert, 2008). Some species occur on shallow reef flats, others in caves on steep reef walls, or at the sand/reef interface at the base of reef slopes. Caves and patches of sand or rubble are particularly favoured habitat by many goby species (Depczynski and Bellwood, 2004). A few goby species, such as *Eviota queenslandica* and *Asterropteryx semipunctata*, are broad habitat generalists that are highly abundant in a range of reef environments (Depczynski and Bellwood, 2004; Hernaman and Probert, 2008). In contrast to the specialist coral-dwelling gobies, the abundances of gobies using these reef habitats is more closely linked to variation in patterns of settlement and post-settlement mortality (Forrester, 1995; Steele and Forrester, 2002; Hernaman and Probert, 2008) than it is to fluctuations in habitat availability.

A considerable number of gobies inhabit soft sediments and rubble beds between reefs, rather than the coral reef itself. Many of these species are cryptically coloured to match the sand and mud backgrounds where they permanently reside. A diverse group of species live in burrows constructed

by alpheid shrimps (Polunin and Lubbock, 1977; Karplus, 1987). Others, such as species of *Amblygobius* and *Valenciennea*, dig their own burrows or hide in crevices and rubble near the reef's edge. Once again, habitat partitioning is observed among these species, with sediment type, depth, and distance from the reef being key environmental variables distinguishing the local-scale distributions of different species (Syms and Jones, 2004; Hernaman and Probert, 2008).

Diets and Feeding

In general, gobies tend to have broad diets and are opportunistic feeders. This applies equally to gobies on coral reefs (Depczynski and Bellwood, 2003; Hernaman *et al.*, 2009), although there are also clear examples of dietary specialization. For example, some species of *Gobiodon* supplement their diet by feeding on the tissue of their coral hosts (Cole *et al.*, 2008; Riedlecker and Herler, 2008) and differences in nutritional value among coral species could potentially explain significant differences in the growth rate and body condition of gobies inhabiting different coral species (Petrie, 2008). Other coral reef gobies have important ecological functions, such as operating as cleaner fish (Taylor and Van Tassell, 2002).

Most coral reef gobies hunt for prey close to the substratum. A few feed in the water column, but always seek shelter in near-by burrows (e.g. ptereleotrine gobies) or the reef matrix (e.g. several *Trimma* species) when threatened (Miller, 1996; Winterbottom and Southcott, 2008). Many of the sand-dwelling species are winnowers, spending much of the day sifting sand through gill rakers to capture small invertebrates (Hernaman *et al.*, 2009). Many cryptic reef gobies feed on meiofauna and small invertebrates that are inaccessible for larger fish and this contributes significantly to energy transfer to higher trophic levels (Depczynski *et al.*, 2007).

In one of the few detailed assessments of the diets of coral reef gobies, Depczynski and Bellwood (2003) showed that many reef gobies are detritivores in addition to carnivores. Most of the smallest goby species (e.g. *Pleurosicya*, *Trimma*, *Eviota* spp.) that they and other authors (Saeki *et al.*, 2005) examined preyed mostly on copepods and other small invertebrates. The intermediate-sized species (e.g. *Istigobius, Asterropteryx, Bathygobius* spp.), however, fed mostly on detrital matter. Three species of *Amblygobius* (*A. rainfordi*, *A. bynoensis* and *A. phalaena*) are herbivores (Depczynski and Bellwood, 2003; Hernaman *et al.*, 2009), feeding mostly on filamentous algae. These results indicate that the diets of coral reef gobies may be more diverse than often assumed.

A study into the feeding habits of five coral reef gobies inhabiting a reef flat at Orpheus Island on the Great Barrier Reef revealed a diverse range of strategies in feeding behaviours (Hernaman *et al.*, 2009). The small cryptobenthic *Asterropteryx semipunctata* was the most generalized feeder, feeding from all available sources (sand patches, detrital algal mats covering rock platforms, algal plants, and the water column), but spending relatively little time on feeding (i.e., mean bite rate of 12.2 bites per ten-minute observation period, and feeding recorded in only 31 % of the observation period). At the other extreme, *Valenciennea muralis* was the most specialized feeder, feeding predominantly (96 % of all bites) by sifting microinvertebrates from sand. Continuous foraging was commonly observed and feeding occupied a large proportion of the activity budget, with a mean feeding rate of 153.9 bites per ten-minute period, and feeding observed in 82 % of the observation period. Whilst invertebrates represent a high quality food resource, high feeding rates might be necessary because of the patchy distribution of microinvertebrates within the sediments, and the high energetic costs and relative inefficiencies associated with the sieving action. Considerable amounts of sedimentary material were ingested during the sieving process (e.g., 24 - 27 % by weight and volume in the gut of *V. muralis*), and high feeding rates may be required to overcome the ingestion of such large amounts of indigestible material.

Predation and Competition

Predation risk is exceptionally high for small fishes on coral reefs (Munday and Jones, 1998) and this likely explains the cryptic life-style of most coral reef gobies. Due to their small size, gobies are preyed upon by a broad suite of predators of all sizes. Even other small fishes that are themselves prey to piscivorous fishes, feed on small gobies that live among the reef matrix. The high risk of predation strongly influences the lifespans and life-history traits of coral reef gobies. High instantaneous mortality rates mean that most coral reef gobies live for less than 1 year on average (Reavis, 1997a; Kritzer, 2002; Hernaman and Munday, 2005a) and some of the smallest species have lifespans of just a few months (Depczynski and Bellwood, 2005, 2006; Winterbottom and Southcott, 2008).

Due to their small size and abundance, gobies have been used by some ecologists to test hypotheses relating to predation and competition in reef fish communities. In an elegant series of experiments, Graham Forrester and Mark Steele demonstrated the importance of shelter availability and predation by larger fishes in controlling the densities of gobies from the

genera *Coryphopterus*, *Gnatholepis* and *Lythrypnus* (Forrester, 1995; Forrester and Steele, 2000, 2004). At the same time, they revealed differences among species in the relative importance of predation and competition in structuring adult populations, and differences in the manner in which mortality was related to population density. In one experiment, newly settled blackeyed gobies *Coryphopterus nicholsii* suffered intense density-dependent predation that dramatically modified patterns of abundance established at settlement (Steele and Forrester, 2002). In contrast, bridled gobies *Coryphopterus glaucofraenum* experienced moderate density-independent predation that only partially modified patterns of abundance established at settlement. Finally, goldspot gobies *Gnatholepis thompsoni* experienced low density-independent predation that did not affect patterns of abundance established at settlement. In another experiment, predation rates on *Coryphopterus glaucofraenum* were density dependent when shelter sites were uncommon, but density-independent when shelter sites were abundant (Forrester and Steele, 2004). These experiments have contributed substantially to our understanding of population regulation in coral reef fishes by demonstrating that the strength of density-dependent mortality can vary greatly among species and locations, and may be associated with the availability of shelter from predators. Competition did not appear to have a significant effect on mortality of these species, but clearly affected growth, which was significantly less at high densities (Forrester *et al.*, 2006).

Predation is greatly reduced in structurally complex habitats, such as among the close-knit branches of coral colonies, and it is here that competition for space becomes the key ecological process. Munday *et al.* (2001) showed that living space is a limited resource for some coral-dwelling gobies and that species compete for access to colonies of preferred coral species, such as *Acropora nasuta*. In lagoons and sheltered reefs, the superior competitors, *Gobiodon histrio* and *G. erythrospilus*, dominate the use of *A. nasuta* and force other species to inhabit alternative coral species (Munday *et al.*, 2001). The ecologically similar *G. histrio* and *G. erythrospilus* also compete for living space, with a lottery for vacant space determined by recruitment dynamics determining the relative abundance of the two species (Munday, 2004a). Competition for space also affects the social and spatial organisation of *G. histrio* and *G. erythrospilus*. Adults of both species form breeding pairs on large coral colonies, and nearly all colonies above a threshold size are occupied by a breeding pair (Hobbs and Munday, 2004). Juveniles are forced to live singly on small corals, but will readily move to form a pair if an adult loses its partner (Hobbs *et al.*, 2004; Wall and Herler, 2008).

Competition for space can have significant consequences for the life histories of coral-dwelling gobies. On the Great Barrier Reef, *G. histrio* and *G. brochus* coexist on the same reefs, but *G. brochus* is rarely able to inhabit colonies of *A. nasuta* because of the dominance of *G. histrio* in this coral. *Gobiodon brochus* is usually found inhabiting colonies of the coral *A. loripes*. However, *G. brochus* individuals inhabiting *A. loripes* grow more slowly and reach a much smaller size compared with individuals inhabiting *A. nasuta* (Munday, 2001). Therefore, competition for space with the dominant competitor, *G. histrio*, affects the maximum size, and ultimately the lifetime fecundity of *G. brochus* (Fig. 4.2.4).

MORPHOLOGY

Morphological Adaptations

Coral reef gobies occupy a wide range of microhabitats, including soft sediments, hard substrates, caves and crevices, and live corals. Accordingly, they exhibit a range of morphological adaptations to these microhabitats, the most obvious being different body shape (Herler, 2007). Most reef gobies, in particular the larger genera that live closely attached to the bottom (e.g., *Istigobius*, *Bathygobius*, *Valenciennea* and *Amblygobius*), have a rather fusiform body shape (Fig. 4.2.1). Other forms, such as the genera *Ptereleotris* and *Nemateleotris*, hover above the bottom and have elongated bodies. In contrast, the forms that live within 3-dimensional structures tend to be compressed (laterally flattened) and those living on surfaces of live corals tend to be depressed (dorso-ventrally flattened) in body shape (Fig. 4.2.5). The best example of highly compressed body shapes are species of the genus *Gobiodon*, some of which are surprisingly large when considering the restricted interbranch spaces offered by their preferred *Acropora* corals (Herler and Hilgers, 2005). One of the largest species *G. histrio* has a highly compressed body, which enables it to move among the coral branches, even when full adult size is attained. In contrast, the smaller *G. rivulatus* has a less compressed body shape, but can still move among the coral branches because of its smaller total body size. The relationship between body shape and habitat use in *Gobiodon* is further illustrated in *G. citrinus*, which inhabit open-branching staghorn corals. *Gobiodon citrinus* grows to a much larger size than *G. histrio*, but has a less compressed body, presumably because its shape is not constrained by coral interbranch space (J. Herler, unpublished data).
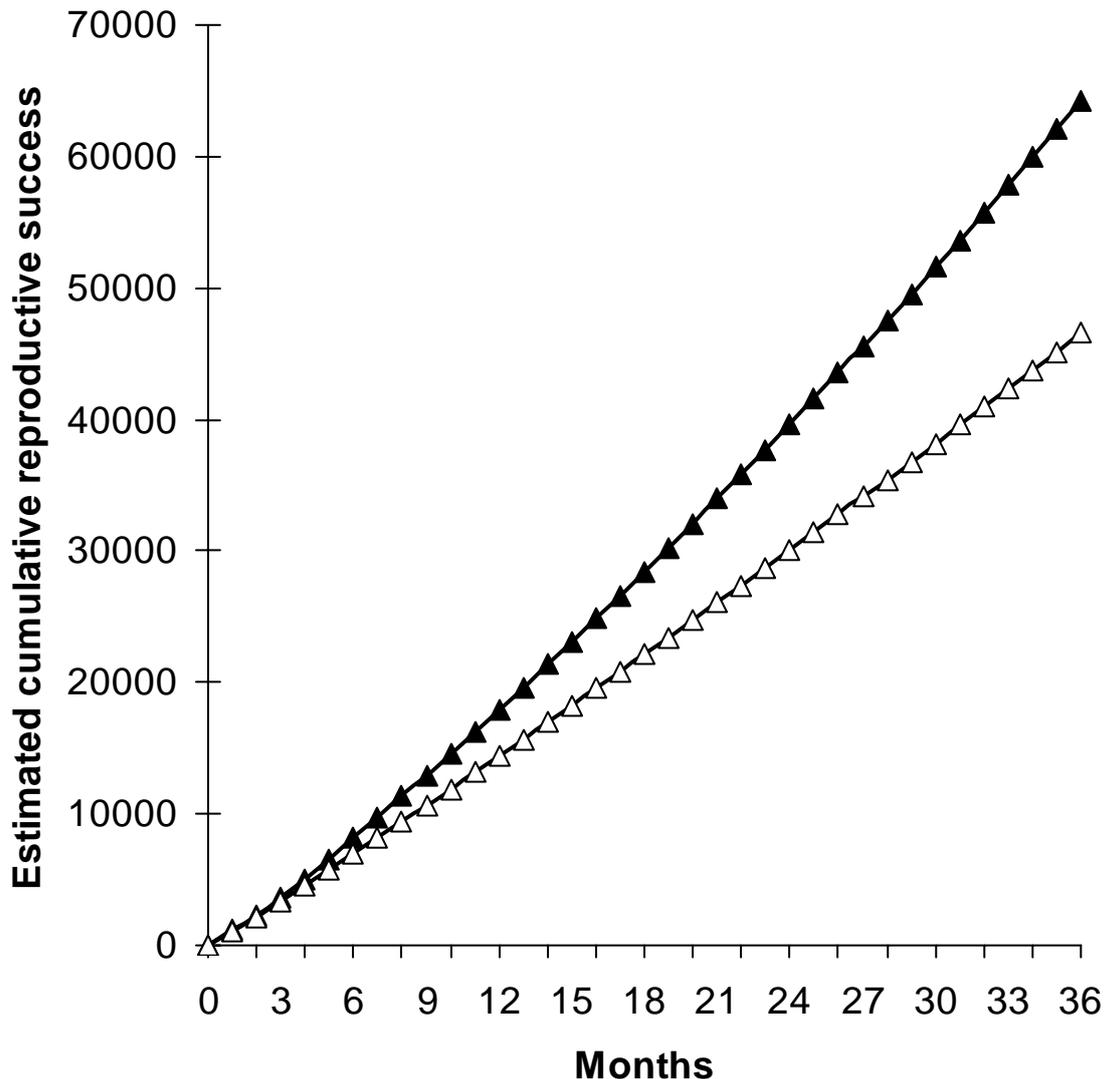
Fig. 4.2.4 Estimated cumulative reproductive success of *Gobiodon brochus* inhabiting either *Acropora nasuta* (filled triangles) or *Acropora loripes* (unfilled triangles). Calculations were based on: 1) age-based growth rates of *G. brochus* inhabiting *A. nasuta* and *A. loripes* reported by Munday (2001), 2) maximum body size of 49 mm for *G. brochus* (P.L. Munday, unpublished data) and 3) the size-fecundity relationships for coral-dwelling gobies reported by Kuwamura *et al.* (1993).

In contrast to species that live in branching corals, gobies that inhabit open surfaces, such as massive and plate-like corals or sea-whips, have depressed bodies to attain close physical contact with the substrate (Fig. 4.2.5). This is exemplified by species such as *Bryaninops yongei*, *B. ridens* and *Pleurosicya micheli* that inhabit seawhips, fire corals and massive scleractinians, respectively, and which are more depressed than con-generic species that inhabit branching corals (Herler, 2007; see also Fig. 4.2.5). Gobies associated with coral rock or caves have a more generalized, typically cylindrical, body form (Herler, 2007).
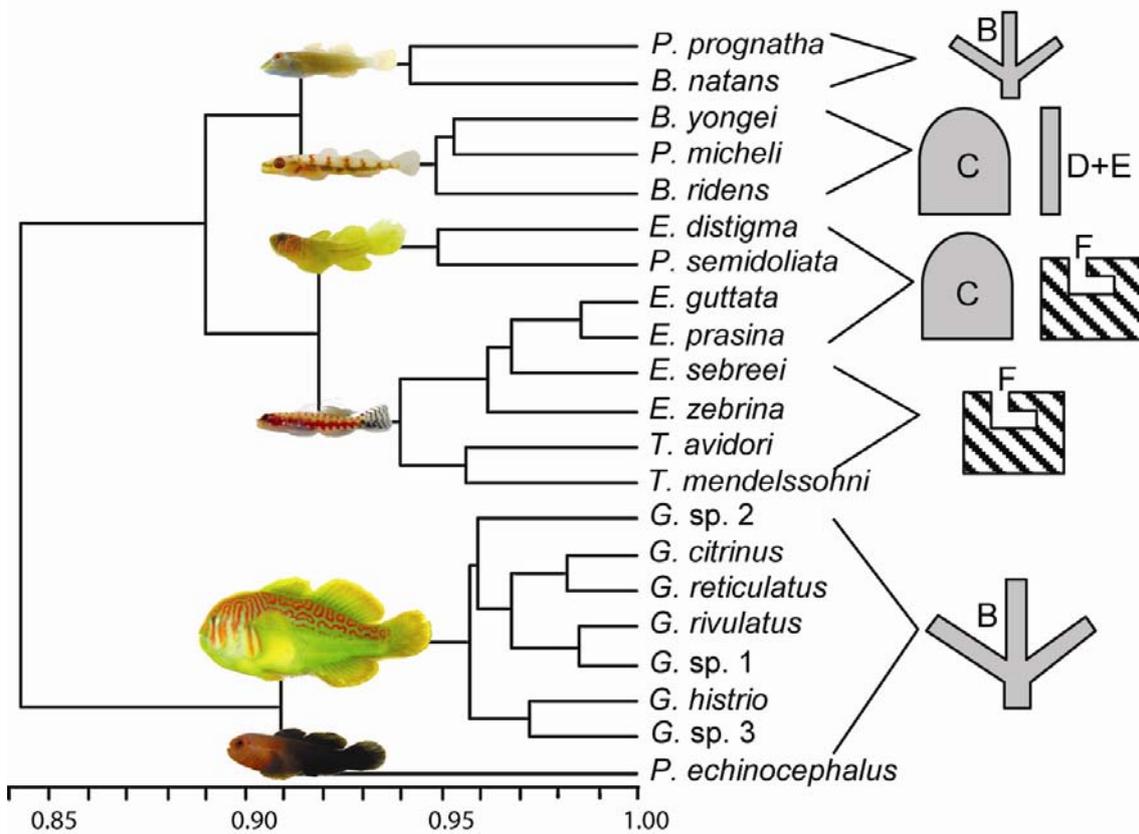
Fig. 4.2.5 Cluster analysis (Bray Curtis – similarity) of nine proportional morphometric variables (all expressed as percent of standard length) of 21 reef gobies from the Gulf of Aqaba, northern Red Sea (modified from Herler, 2007). The most frequented microhabitats are indicated (B = branching corals, C = massive corals, D = *Millepora dichotoma*, E = *Cirripathes* sp., F = coral rock). Fish genera abbreviations: B = *Bryaninops*, E = *Eviota*, G = *Gobiodon*, P = *Paragobiodon* (*echinocephalus*), *Pleurosicya* (*prognatha* and *micheli*), *Priolepis* (*semidoliata*), and T = *Trimma* respectively.

In addition to overall body form, the morphology of fins is often associated with the preferred microhabitat. A common feature of gobies is united pelvic fins, forming a pelvic disc. Advanced developmental states of the pelvic disc are present in *Bryaninops*, *Pleurosicya*, *Gobiodon* and *Paragobiodon*, all of which inhabit live coral. In these species the pelvic fins form cup-shaped sucking discs. The two former genera comprise the most advanced state by having a lobed anterior frenum that is folded anteriorly to form a pocket-like structure (Larson, 1985, 1990; Herler, 2007). In contrast, coral-rock dwelling gobies have fins that may be united but are neither disc- or cup-shaped, nor with an anterior frenum (e.g. *Trimma* and *Priolepis*), or have almost separate fins (e.g. *Eviota*) (Herler, 2007). This suggests that a sucking disc is most useful on a smooth substrate, such as the surface of

live corals, whereas, on rock or other rough substrate, a sucking function may not be possible. The pectoral fin might also play a role for locomotion within coral branches. Some species of *Gobiodon* have a wide pectoral fin base, which supports strong pectoral fin propulsion (J. Herler, unpublished data).

Apart from body form adaptation that may optimize locomotion and minimize predation risk, another adaptative feature that has likely evolved in response to the high predation is toxic skin mucous in the genus *Gobiodon* (Schubert *et al.*, 2003). Chemical alarm cues, which have been discovered in the small reef goby *Asterropteryx semipunctata* (McCormick and Larson, 2007), could also help reduce the risk of predation in coral reef gobies.

Morphological and Functional Consequences of Size Diminution

Miniaturization is the evolution of extremely small body size within a phylogenetic lineage (Hanken and Wake (1993). Gobies in general are a group of small fishes, with the majority being less than 10 cm (Larson and Murdy, 2001), and therefore, were good candidates for miniaturization. On coral reefs we find a unique diversity of small goby species that often do not exceed 3 cm maximum adult size. Spatial restriction of habitats has promoted miniaturization in some animal groups (Hanken and Wake, 1993). Such habitats are particularly diverse in coral reefs and may explain the diversity of small gobies in this ecosystem. Miniature gobies mostly occupy corals and coral-rock crevices, where they presumably gain better shelter from predators.

While the reduction of size was probably important for access to small shelter sites where predation risk is minimal, diminution has also had important consequences for the anatomy, ecology, physiology, and life histories of coral reef gobies (Miller, 1996; Munday and Jones, 1998). In reef gobies, size diminution and short lifespans may have been important promotors for reductions of squamation, locomotory body parts, and sensory systems. Scales are usually reduced in the smaller and/or more cryptic genera such as *Bryaninops*, *Eviota*, *Trimma* and *Trimmatom* (Winterbottom, 1990; Herler and Hilgers, 2005). At the extreme, scales are completely absent in the tiny *Trimmatom sagma*, *T. officius* and *T. nanus* (Winterbottom, 1990). Scales are also absent in the coral-dwelling *Gobiodon* (Herler and Hilgers, 2005; Harold *et al.*, 2008), but here squamation is replaced by a thick skin

mucus layer that contains toxic substances and may prevent predation or parasite infestation (Munday *et al.*, 2003; Schubert *et al.*, 2003).

Reductions of fins in reef gobies involves the loss of fin-ray branching, or loss of entire rays in the median and pectoral fins (e.g., Lachner and Karnella, 1980; Larson, 1985, 1990; Winterbottom, 1990). Also the pelvic fin is often reduced: the fifth ray may be very short or almost absent (e.g. several species of *Eviota* and *Trimmatom*) (Lachner and Karnella, 1980; Winterbottom, 1990), resulting in the loss of pelvic sucking function (Herler, 2007). The supporting skeletal elements, such as the pterygiophores of median fins or the radials and scapula that support the pectoral fin, are often reduced or lack ossification in these tiny gobies (Winterbottom, 1990). These reductions were likely promoted by a cryptic life-style in spatially restricted habitats, where swimming may not be necessary, or possible. Similarly, a cryptic life-style may have reduced the importance of the lateral line system and promoted reductions in its development. In the genera *Priolepis*, *Trimma* and *Trimmatom* for example, head sensory canals have been lost and even the usually numerous rows of superficial head neuromasts may be reduced in number (Winterbottom, 1990, 2006).

Other important morphological changes associated with size reduction are caused by functional constraints of organs that do not proportionately follow overall body diminution. For example, relative eye size is greater in minute fish (Herler, 2007) due to physical constraints of eye development (Kirschfeld, 1976). This leads to disproportionate size development of head skeleton regions and can even affect trophic morphological structures. For example, Riedlecker and Herler (2008) found that eye size influences jaw suspensorium shape in different species of *Gobiodon*. Deeper-water species with large eyes had smaller suspensoria and a lower suspensorium/jaw-articulation angle than did shallow water species with smaller eyes. This may have important consequences for diet and feeding function.

Another important constraint set by diminution of body size is the limitation of bestowal and fecundity in small gobies. Although goby eggs are relatively small (Miller, 1979; Miller, 1996), life-time fecundity may be as little as several hundred eggs per female in the smallest species of *Eviota* (Depczynski and Bellwood, 2005). This has important consequences for population dynamics because any alteration of mortality rates will impact population sizes immediately due to their short adult lifespan and reproductive period. Behavioral adaptations that may partly compensate for low fecundity levels include egg guarding and egg fanning to increase oxygen supply (Depczynski and Bellwood, 2005).

LIFE HISTORY

Many small species of coral reef fishes are surprisingly long-lived, e.g., 18 - 32 years for several damselfishes (Worthington *et al.*, 1995; Meekan *et al.*, 2001) and 25 - 30 years for some small surgeonfishes (Choat and Axe, 1996; Hart and Russ, 1996; Choat and Robertson, 2002). These long-lived species tend to attain an asymptotic size very quickly (within 2 - 6 years) and thus spend much of their lifespan (often > 75 %) at that size. In contrast, the life history patterns of coral reef gobies are typified by short lives and continued investment in growth for all or much of the lifespan. High mortality rates and short adult lifespans are important selection pressures influencing the timing of maturation and reproductive output in coral reef gobies.

Mortality and Longevity

Most coral reef gobies are short-lived, with maximum lifespans in the order of 2 - 4 years for the coral-dwelling species (Kuwamura *et al.*, 1996; Munday, 2001), 1 - 2 years for the cryptobenthic and burrow-dwelling species (Yanagisawa, 1982; Forrester, 1995; Reavis and Barlow, 1998; Kritzer, 2002; Hernaman and Munday, 2005a), and just 2 - 3 months for the smallest reef-dwelling species (Depczynski and Bellwood, 2006; Winterbottom and Southcott, 2008). *Eviota sigillata* reaches a maximum total length (TL) of 20 mm and has a maximum lifespan of just 8 weeks, making it the shortest recorded lifespan of any vertebrate (Depczynski and Bellwood, 2005). The similarly-sized *Trimma nasa* is also extremely short-lived, with a maximum lifespan of 12 weeks (Winterbottom and Southcott, 2008). These species experience extremely high daily mortality rates of 5 - 8 %. Larger species (50 - 120 mm TL) that live in burrows (*Valenciennea muralis*, *Amblygobius bynoensis*, and *Amblygobius phalaena*) or cryptically amongst algal-covered rubble (*Asterropteryx semipunctata*) and rocks (*Istigobius goldmanni*) have slightly lower daily mortality rates (~ 1 %), but are still relatively short-lived with maximum lifespans of 11 - 16 months (Hernaman and Munday, 2005a). Coral reef gobies are preyed upon by a wide range of reef fishes, including scorpaenids, muraenids, pinguipedids, synodontids and serranids (Luckhurst and Luckhurst, 1977; Sweatman, 1984; Parrish *et al.*, 1986; Norris and Parrish, 1988; Forrester, 1995). Predation probably accounts for much of the high mortality rates experienced by the cryptobenthic and burrow-dwelling species that must venture from their shelter site to feed, or, for females of the many polygynous species, to visit a nesting site to spawn. In contrast, coral-dwelling gobies do not need to leave their coral host to

feed or mate, and the longer lifespans of these species may be related to the increased protection from predation afforded by the branches of the host coral colony.

Life History Patterns and the Timing of Maturation

The most extreme life history is exhibited by the coral reef pygmy goby *Eviota sigillata*, which settles from the plankton after 3 weeks, matures within 1 - 2 weeks of settlement, and has a maximum adult lifespan of less than 4 weeks. A similar life history is exhibited by the equally small *Trimma nasa*, which has a maximum of 7 weeks following settlement in which to grow, mature and reproduce. Such shortened lifespans heavily affect the benthic part of the life cycle by severely reducing the time available for maturation and reproductive events. They do not, however, appear to affect the pelagic part of the life cycle, with pelagic larval duration (PLD; the time between hatching and settlement to the adult habitat) being within the range exhibited by many goby species from a variety of habitats (Table 4.2.1). For *Trimma nasa* and species of *Eviota*, the PLD is 39 - 42 % of the maximum lifespan. This compares to 6 - 11 % for cryptobenthic and burrow-dwelling gobies (Table 4.2.1). In contrast, the PLDs of most reef fish species typically comprise < 1 % of their expected lifespan (Depczynski and Bellwood, 2006). The observation that the PLD of extremely short-lived species is similar to longer-lived gobies indicates that there may be an optimal size/age at which fish larvae can successfully settle onto the reef habitat or that morphological and physiological development of larval gobies is constrained to a certain timeframe.

Life history theory predicts that high adult mortality will select for early maturation, which results in a higher probability of survival to first reproduction, shorter generation times, and a higher instantaneous rate of natural increase (Begon and Mortimer, 1981; Stearns, 1992). Hernaman and Munday (2005b) examined the timing of maturation in five goby species that experienced annual mortality rates of >97 %. Males of all five species and females of three species matured at a smaller size (relative to their mean maximum size) than is typically found for fishes, indicating selection for relatively early maturation. Mean size at maturation ranged from 50 - 60 % of maximum size for females, and 41 - 52 % for males (depending on species). Thus, males of all five species not only matured at a considerably smaller relative size than expected from life history patterns for fishes (65 %; Charnov, 1993), but also at or below the lower threshold for organisms in general (50 - 80 %; Charnov, 1993). A similar result was

Table 4.2.1 Mean size and age at settlement for coral reef gobies from a range of habitat types (SL, standard length; TL, total length; -- data unavailable)

Habitat	Species	Mean PLD (days)	% of max. age represented by PLD (%)	Mean size at settlement (mm)	Source
Cryptobenthic /epibenthic	*Eviota queenslandica*	24.2	24	7-7.5 TL	Depczynski & Bellwood (2006)
	Eviota sigillata	24.7	42	7-7.5 TL	Depczynski & Bellwood (2006)
	Istigobius goldmanni	25.7	7	8.1 TL	Hernaman (2003)
	Eviota melasma	26.2	27	7-7.5 TL	Depczynski & Bellwood (2006)
	Coryphopterus glaucofraenum	26.8	--	6.4 SL	Sponaugle & Cowen (1994)
	Asterropteryx semipunctata	27.5	6	7.6 TL	Hernaman (2003)
	Trimma nasa	33.9	39	--	Winterbottom & Southcott (2008)
Burrow-dwellers	*Amblygobius bynoensis*	28.2	8	10.1 TL	Hernaman (2003)
	Amblygobius phalaena	32.8	8	11.8 TL	Hernaman (2003)
	Valenciennea muralis	39.5	11	11.3 TL	Hernaman (2003)
	Amblygobius rainfordi	40.3	--	14.4 SL	Brothers *et al.* (1983)
Coral-dwellers	*Gobiodon erythrospilus*	17.6	<2	--	Munday & Hernaman, unpublished data
	Gobiodon histrio	21.2	<2	--	Munday & Hernaman, unpublished data
	Paragobiodon xanthosomus	23.0	--	--	Munday & Hernaman, unpublished data

found for females of the short-lived *Eviota queenslandica* and *E. melasma*, which on average matured at 51 % and 44 % of their mean maximum size respectively (Depczynski and Bellwood, 2006).

Although high adult mortality appears to have favoured early maturation in some species, not all gobies mature at such small relative sizes. Female *Asterropteryx semipunctata*, *Istigobius goldmanni*, and even the tiny *Eviota sigillata*, mature at around 63 - 65 % of their mean maximum size (Hernaman and Munday, 2005b; Depczynski and Bellwood, 2006). The relatively larger size at maturation of these species may be associated with physiological constraints of a very small body size (*E. sigillata*) and the competitive benefits associated with a larger body size in polygynous species (*A. semipunctata* and *I. goldmanni*). The size at maturation (11 mm) of *Eviota sigillata* is very close to the physiological threshold at which maturation can occur (~10 mm; an exception may be *Trimmatom nanus*, which matures at 8 mm (Winterbottom, 1990)). The mean size at maturity for female *A. semipunctata* (27.7 mm TL) and *I. goldmanni* (30.7 mm TL) is 18 - 21 mm larger than the minimum size threshold of 10 mm. However, these species are much longer lived than *Eviota* and maturation may be delayed to obtain reproductive and competitive benefits associated with a larger body size. Both species are polygynous and tend to be found in high densities (Hernaman and Munday, 2007; Hernaman and Probert, 2008). The benefits associated with a large body size, in terms of increased fecundity and enhanced success in competition for shelter and spawning sites, may select against very early maturation in these species.

Seasonal influences on growth rates can also modify the timing of maturation. Hernaman and Munday (2005a) detected seasonal differences in growth rates for adults and juveniles of four goby species from three genera (*Valenciennea*, *Amblygobius* and *Istigobius*). Summer-growing individuals had significantly higher growth rates than winter-growing individuals, which had a considerable impact on the age at first reproduction by influencing the time required to attain a size suitable for maturation. Winter- and summer-growing *V. muralis* and *A. bynoensis* females matured at the same mean size, but due to seasonal differences in growth rates, summer fish attained that size one month quicker and thus matured at a significantly younger age than winter fish. This has important implications for short-lived coral reef species with seasonal reproduction, and suggests that the season of settlement may have a significant impact on the timing of maturation, the probability of survival to maturation, and reproductive success.

Patterns of Growth

Coral reef gobies typically invest in somatic growth throughout much or all of their lifespan, spending relatively little or no time at asymptotic size (e.g., Hernaman and Munday, 2005a; see also Fig. 4.2.6). Rapid near-linear growth has also been recorded in some species, including *Istigobius decoratus* (Kritzer, 2002), *I. goldmanni* (Hernaman and Munday, 2005a), *Trimma nasa* (Winterbottom and Southcott, 2008), and three species of *Eviota* (Depczynski and Bellwood, 2006). Similarly, the intertidal Hawaiian goby, *Bathygobius coalitus*, exhibited a linear pattern of growth for at least the first nine months of life, with no difference in growth rate between immature and mature gobies (Shafer, 1998).

The growth pattern of most coral reef gobies differs considerably to that exhibited by other relatively small, but long-lived coral reef fishes, such as certain acanthurids (e.g., Choat and Axe, 1996; Hart and Russ, 1996) and pomacentrids (e.g., Meekan *et al.*, 2001). These long-lived species often have a growth pattern characterized by rapid growth to asymptotic size and sexual maturity, followed by a relatively long period of reproductive activity but little additional somatic growth (Choat and Robertson, 2002). This growth pattern may reflect a physiological trade-off between growth and reproduction. Trade-offs play a central role in life history theory, and a physiological trade-off between growth and reproduction is expected where these two processes compete directly for a limited amount of energy (Begon and Mortimer, 1981; Partridge and Harvey, 1988; Stearns, 1992). Coral reef gobies are apparently able to acquire sufficient energy to satisfy demands for both growth and reproduction, with no apparent trade-off between these traits. However, this capacity to continue somatic growth throughout life may come at a cost of reduced longevity, possible due to increased exposure to predators while feeding to maintain sufficient energy to support rapid growth and high reproductive effort.

SOCIAL ORGANISATION AND REPRODUCTIVE STRATEGIES

In common with other gobies, coral reef species are demersal spawners with paternal egg care (Thresher, 1984). Resource defense polygyny, where males defend a nesting site that is visited by females, appears to be a common form of social organisation for coral reef gobies (e.g., Sunobe and Nakazono, 1990; Black *et al.*, 2005; Manabe *et al.*, 2007b; Manabe *et al.*, 2009) especially among species that live at high density populations (Hernaman and
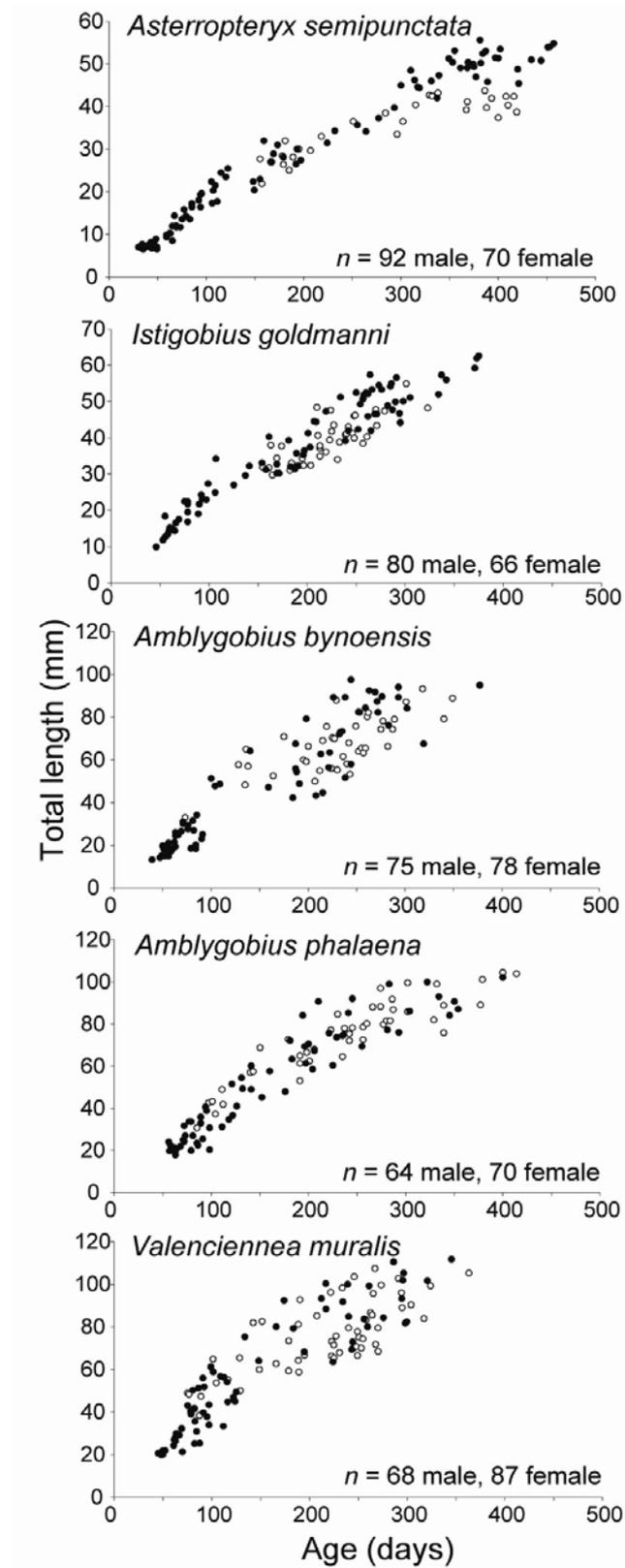
Fig. 4.2.6 Growth trajectories for five species of coral reef goby (males, filled circles; females, open circles. Unsexed juveniles used in both male and female data sets). Modified from Hernaman and Munday (2005a).

Munday, 2007). In contrast, pair-forming is common among species that live in low densities on sediments and rubble (e.g., Reavis, 1997b; Takegaki and Nakazono, 1999; Takegaki, 2000; Hernaman and Munday, 2007) and is the usual social structure of shrimp-associated gobies (Yanagisawa, 1982). These pair bonds are typically long-lasting and monogamous (Whiteman and Cote, 2004). Monogamy also occurs among obligate coral-dwelling gobies, but here it may be associated with social groups ranging in size from pairs up to 10 or more individuals (e.g., Kuwamura *et al.*, 1994; Munday *et al.*, 1998; Munday *et al.*, 2002; Thompson *et al.*, 2007). The presence of monogamy in large social groups increases the opportunities for conflict among individuals and has led to the evolution of complex behaviours to maintain social order within these goby societies (Wong *et al.*, 2007).

The most complex social structures are exhibited by group-forming species such as *Paragobiodon xanthosomus*. This species forms groups of up to 10 or more individuals on a single coral head, but only the two largest individuals are reproductively mature and they form a size-matched breeding pair. The presence of the dominant female keeps all the subordinate fish from becoming reproductively mature (Wong *et al.*, 2008a). Subordinates queue to reach the breeding positions, with the stability of the queue maintained by a strict size-based hierarchy. Each individual in the queue has a body-size ratio of approximately 90 - 95 % of its immediate dominant. Any individual that tries to advance its position in the queue by increasing its size will be evicted from the group when the body-size ratio between itself and its immediate dominant exceeds the threshold for conflict between the two ranks (Wong *et al.*, 2007). Remarkably, individuals control their own growth rate so that they do not exceed this critical size threshold, and they can do this by regulating their dietary intake (Wong *et al.*, 2008b). However, if the dominant dies or is removed the subordinate will rapidly accelerate its growth until it reaches the size threshold with the next higher individual in the queue (Wong *et al.*, 2007). Similar control of individual growth rates has been observed in the pair-forming *G. histrio*, where males and females will adjust their growth rates to maintain a size-matched breeding pair (Munday *et al.*, 2006b).

Group size of *P. xanthosomus*, and some other coral-dwelling gobies, is influenced by the size of the coral host, with larger groups inhabiting larger coral colonies (Thompson *et al.*, 2007). Other species are strictly pair-forming regardless of coral colony size and the resident pair defend their host coral from any intruders (Munday *et al.*, 1998; Hobbs and Munday, 2004; Thompson *et al.*, 2007). Juveniles usually inhabit small coral colonies that are not big enough for breeding pairs. These juveniles will readily

move to establish a pair with a single adult on a larger coral if there is an opportunity to do so. Juveniles delay maturation until they are able to form a pair, and then they rapidly mature into the opposite sex of the single adult (Kuwamura *et al.*, 1996; Hobbs *et al.*, 2004). Presumably delaying maturation allows juvenile gobies to invest additional energy in growth and also ensures they can mature into the correct sex to match available breeding opportunities (Hobbs *et al.*, 2004).

Alternative male mating tactics have been identified in several species, with small males either attempting to sneak spawn or intercept females before they reach the nesting sites of larger males (Sunobe and Nakazono, 1999a; Drilling and Grober, 2005; Manabe *et al.*, 2009). Perhaps the most intriguing reproductive characteristic of coral reef gobies, however, is the capacity of many species to change sex, in some cases more than once (e.g. Sunobe and Nakazono, 1993; Kuwamura *et al.*, 1994; Nakashima *et al.*, 1996; Munday *et al.*, 1998). Although many species are gonochoristic, many others are hermaphroditic, with the presence of gonochorism and hermaphroditism tending to be conserved within genera (Cole, 1990). At least 14 genera of gobies are confirmed to have hermaphroditic species, or are expected to be hermaphroditic based on behaviour or gonadal characteristics (de Mitcheson and Liu, 2008). Most of these species are found on or near coral reefs. In contrast, only a handful of temperate marine gobies are known to be hermaphroditic (e.g., Cole, 1983; Cole, 1990; St. Mary, 1996, 2000). Sex change is not known from freshwater species (de Mitcheson and Liu, 2008).

Sex change from female to male (protogyny) is exhibited by a number of species with a polygynous mating system (e.g. Cole and Robertson, 1988; Cole and Shapiro, 1992; Sunobe and Nakazono, 1999b). These species typically have a female biased sex ratio and the largest individual in a social group is male. Protogynous sex change can be favoured in a polygynous mating system because male reproductive success often increases more steeply with size or age than does the female reproductive success in this mating system. Therefore, an individual can maximize its lifetime reproductive success by first reproducing as a female and then changing sex to male when large enough to defend a nest site that is visited by multiple females (Munday *et al.*, 2006a). Intriguingly, there are many goby species with polygynous mating systems that do not change sex. It is unknown if phylogenetic constraints have prevented the evolution of sex change in these species, or there are some ecological characteristics that favour gonochorism over hermaphroditism in the species (Cole, 1990; de Mitcheson and Liu, 2008).

An increasing number of coral reef gobies are now recognized as being capable of bi-directional sex change (Munday *et al.*, 2010). In these species both males and females can change sex, and individuals may change sex more than once. Bi-directional sex change occurs in two different circumstances. In some polygynous gobies, such as *Trimma okinawae*, females change sex to males when there is the opportunity to defend a harem of females (Sunobe and Nakazono, 1990). Males may change sex back to female if they become single and the only breeding opportunity immediately available to them is to join another social group. They will change sex and reproduce as a female if they are smaller than the resident male in the new social group (Manabe *et al.*, 2007a, 2007b). The advantage to sex change by males may lie in the fact that these small gobies experience high and unpredictable rates of mortality. On average a single male may have higher reproductive success by changing sex and reproducing as a female in a new harem than if he remains male and waits for a new harem to form (Munday *et al.*, 2006a).

Bi-directional sex change is also common among coral-dwelling gobies that form monogamous pairs (Kuwamura *et al.*, 1994; Nakashima *et al.*, 1996; Munday *et al.*, 1998). Here the advantage of sex change appears to be that there are very few single adults in the population and the ability to change sex in either direction reduces the risk of searching for a new mate, because a single adult could form a new breeding pair with any other single adult encountered (Nakashima *et al.*, 1996; Munday *et al.*, 2010). The common threads that link bi-directional sex change in polygynous and pair-forming species are the unpredictability of alternative mating opportunities for single fish and the high risk of predation in searching for new mates due to the small body size of gobies.

CONSERVATION

Coral reefs are under increasing stress from a variety of threats, including terrestrial pollution and runoff, overfishing, and climate change (Hughes *et al.*, 2003). Coral cover has declined on reefs in many parts of the world and in some locations a substantial proportion of reefs are already considered to be seriously degraded (Wilkinson, 2008). The relatively high abundance and short generation time of most coral reef gobies are characteristics that usually confer resilience to disturbance (Dulvy *et al.*, 2003). Many goby species are also geographically widespread, which greatly reduces their risk of extinction. The threat to goby species from degrading reef habitat will, therefore, mostly depend on their patterns of habitat use.

Species that utilize sand patches, rubble, or dead coral matrix may increase in abundance as these habitats become ubiquitous on degraded reefs. In contrast, populations of coral-dwelling species rapidly decline in abundance following coral loss (Munday *et al.*, 1997; Munday, 2004b; Pratchett *et al.*, 2008). Continued degradation of coral reef habitat will therefore cause shifts to goby community structure, towards communities with fewer coral specialists and more non-coral generalists. In an example of this shift in structure, Bellwood *et al.* (2006) showed that sand and rubble-dwelling gobies, such as *Eviota queenslandica* and several *Istigobius* species, increased in abundance following a major bleaching event, whereas coral-dwelling *Gobiodon* and *Paragobiodon* species disappeared or became uncommon.

Although some goby species will be favoured by the continued degradation of coral reef habitat, the net effect on the diversity of coral reef gobies is expected to be negative because a considerable number of species rely on living corals (e.g. species of *Gobiodon*, *Paragobiodon*, *Bryaninops*, *Pleurosicya* and some *Eviota* species) or other healthy invertebrate assemblages (e.g some species of *Pleurosicya*, *Luposicya* and *Gobiosoma*) for their survival. As healthy coral and benthic invertebrate communities decline, so too will the abundance of the many goby species that use these organisms as habitat. Furthermore, the species of *Acropora* and *Pocillopora* corals preferred by many coral-dwelling gobies are also the ones that are most susceptible to thermally-induced coral bleaching (Pratchett *et al.*, 2008). Therefore, the effects of global warming might be particularly severe for coral-dwelling gobies.

Even among coral-dwelling species, it appears that specialist species suffer more than generalist species from coral declines. Munday (2004b) found that populations of *Gobiodon* species that inhabit just one or two species of coral declined in abundance proportionally more than *Gobiodon* species that inhabit many coral species (Fig. 4.2.3). In addition, the specialist species had smaller population sizes before the disturbance (Munday, 2004b). Therefore, the specialist coral-dwellers were especially prone to local extinction because they had both smaller populations before the disturbance and larger percentage declines as a result of the disturbance. Although most coral-dwelling gobies have large geographic ranges (Munday *et al.*, 1999; Herler *et al.*, 2009), and are thus unlikely to be at risk of global extinction due to the effects of sporadic local extinctions, there are a few species of *Gobiodon* that appear to have very small geographic ranges (Munday *et al.*, 1999; Munday, 2004b; Herler and Hilgers, 2005; Herler *et al.*, 2009). The combination of specialization on live coral habitat, relatively small population sizes, and small geographic range, places

these species at a greater risk of extinction than most other coral reef fishes (Munday, 2004b). Consequently, some of these small-range, coral-dwelling gobies may be among the most threatened of coral reef fishes.

CONCLUSIONS

The Gobiidae is the most species-rich family of coral reef fishes, yet many species still remain to be discovered or described. The small body size of most reef gobies makes them prone to predation and requires them to live cryptically. They occupy almost every type of microhabitat associated with coral reefs, including soft sediments, coral rock and rubble, caves and crevices, and even the burrows of shrimps. Many species use other reef organisms as habitat, especially scleractinian corals, to which some have evolved species-specific relationships. The different degrees of microhabitat specialization exhibited by coral reef gobies have implications for their distribution and abundance within and among reefs. The close association with coral habitats has also resulted in numerous morphological and behavioural adaptations, some of which are unique among reef fishes. The evolution of bi-directional sex change, cooperative growth regulation, hypoxia tolerance, skin toxins and various morphological characters is closely linked to microhabitat specialization, while morphological reductions characterize many of the smaller reef goby genera.

Evolutionary size diminution increases the risk of predation and this important source of mortality appears to have been a key factor shaping the life histories of coral reef gobies. High mortality rates mean that most reef gobies are short-lived. Many species live for a maximum of 1 - 2 years, while the smallest species may live just 1 - 2 months. Unlike most other coral reef fishes, gobies tend to exhibit continuous growth throughout life. At the same time they tend to mature early and exhibit high reproductive effort. Fast growth, early maturation and high reproductive effort are all characteristic of species with high mortality rates. Some coral-dwelling species are longer lived, presumably because they gain protection from predators by living among the close-knit branches of coral colonies. The use of coral habitat shelters individuals from predators, but it increases the intensity of competition for shelter space. In these species, intra- and interspecific competition for shelter space influences patterns of habitat use, local distributions and abundances, growth rates and survival. Habitat specialization and associated ecological adaptations also appear to have promoted species diversification in these coral-dwelling gobies.

Their high abundance and fast population turn-over mean that gobies play an important role in energy transfer through coral reef communities. The many planktivorous, micro-carnivorous and detritivorous species provide important linkages to higher trophic levels. In turn, many reef gobies – in particular those that are associated with live coral or other benthic invertebrates – depend on healthy reefs for their continued persistence. With coral reefs in decline due to various local and global anthropogenic stresses, we expect to observe shifts in the community structure of coral reef gobies over coming decades. Many of the highly specialist coral-dwelling species will decline in abundance, with a few species facing an elevated risk of extinction. In contrast, some generalist, rock, sand and rubble dwelling species may become more ubiquitous.

In this chapter we have demonstrated that, despite often being neglected in studies of reef fish assemblages, coral reef gobies are not only an ecologically important component of reef systems but are also good research models. Their exceptional species richness and widespread distribution offer excellent opportunities for investigating mechanisms of species diversification and maintenance of species diversity. Their small size and robust nature makes them well-suited to experimental manipulation, with recent experiments using gobies as model species making significant contributions to our understanding of how reef fish communities are structured and their populations regulated. As the smallest and shortest-living vertebrates they are critically important for understanding the evolution of animal life-history traits and for explaining scaling relationships of life history traits among species.

Acknowledgements

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