



# Drivers of sociality in *Gobiodon* fishes: An assessment of phylogeny, ecology and life-history



Martin L. Hing<sup>a,\*</sup>, O. Selma Klanten<sup>b</sup>, Marian Y.L. Wong<sup>a</sup>, Mark Dowton<sup>c</sup>

<sup>a</sup> Centre for Sustainable Ecosystems Solutions, School of Earth, Atmospheric and Life Sciences, University of Wollongong, Australia

<sup>b</sup> Fish Ecology Laboratory, School of Life Sciences, University of Technology Sydney, Australia

<sup>c</sup> Molecular Horizons, School of Chemistry and Molecular Bioscience, University of Wollongong, Australia

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## ABSTRACT

What drives the evolution of sociality in animals? Many robust studies in terrestrial organisms have pointed toward various kinship-based, ecological and life-history traits or phylogenetic constraint which have played a role in the evolution of sociality. These traits are not mutually exclusive and the exact combination of traits is likely taxon-specific. Phylogenetic comparative analyses have been instrumental in identifying social lineages and comparing various traits with non-social lineages to give broad evolutionary perspectives on the development of sociality. Few studies have attempted this approach in marine vertebrate systems. Social marine fishes are particularly interesting because many have a pelagic larval phase and non-conventional life-history strategies (e.g. bi-directional sex-change) not often observed in terrestrial animals. Such strategies provide novel insights into terrestrially-derived theories of social evolution. Here, **we assess the strength of the phylogenetic signal of sociality in the *Gobiodon* genus with Pagel's lambda and Blomberg's K parameters.** We found some evidence of a phylogenetic signal of sociality, but factors other than phylogenetic constraint also have a strong influence on the extant social state of each species. We then use phylogenetic generalized least squares analyses to examine several ecological and life-history traits that may have influenced the evolution of sociality in the genus. We found an interaction of habitat size and fish length was the strongest predictor of sociality. Sociality in larger species was more dependent on coral size than in smaller species, but smaller species were more social overall, regardless of coral size. Finally, we comment on findings regarding the validity of the species *G. spilophthalmus* which arose during the course of our research. These findings in a group of marine fishes add a unique perspective on the evolution of sociality to the excellent terrestrial work conducted in this field.

## 1. Introduction

The question of how sociality first arose in animals has attracted much attention in the fields of evolutionary ecology and animal behaviour. Many mechanisms are thought to contribute to the evolution of sociality including ecological factors, life-history traits and phylogeny (Arnold and Owens, 1998; Emlen, 1982; Hamilton, 1964; Hatchwell and Komdeur, 2000; reviewed in Hing et al., 2017; Kokko and Ekman, 2002). These features are not mutually exclusive and may be highly dependent on each other (Arnold and Owens, 1998; Chapple, 2003). Hamilton's rule predicts that sociality should evolve under certain combinations of relatedness and costs and benefits of social actions and is widely regarded as a universal framework to study social evolution (Bourke, 2014; Hamilton, 1964). Ecology, life-history and relatedness change the costs and benefits conferred to individuals within the group.

Under this framework, individuals should receive greater inclusive fitness benefits if they form social groups with close relatives (Briga et al., 2012; Hughes et al., 2008). Groups consisting of unrelated individuals are also possible if ecological or life-history factors alter the direct costs and benefits of group living such that the benefits outweigh the costs (e.g. Buston et al., 2007; Riehl, 2011).

Phylogenetic relationships among taxa can constrain the evolution of sociality which may predispose species to sociality (e.g. Agnarsson, 2002; Nowicki et al., 2018; Schneider and Kappeler, 2014; Smorkatcheva and Lukhtanov, 2014). However, the extant state of sociality may depend on various ecological and life-history conditions (Chapple, 2003; Rubenstein and Lovette, 2007; Schürch et al., 2016). For example, altered environmental conditions and extreme weather events could reduce habitat sizes for a normally social species, increasing animal density and increasing conflict within the group

\* Corresponding author.

E-mail address: [martinhing@gmail.com](mailto:martinhing@gmail.com) (M.L. Hing).

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ultimately leading to a reduction in sociality (Hing et al., 2018). On the other hand, some species in which sociality has a strong phylogenetic signal (that is, sociality is highly constrained), may maintain their sociality regardless of other factors (Kruckenhauser et al., 1999; Nowicki et al., 2018; Shultz et al., 2011). In either case, understanding the strength of the relationship between phylogeny and sociality can help us to understand what role phylogeny played in the evolution of sociality.

The majority of studies of sociality have been conducted on birds, mammals and invertebrates wherein subordinates are usually related to dominants and display natal philopatry (Bourke, 2011; Hing et al., 2017; Jennions and Macdonald, 1994; Jetz and Rubenstein, 2011; Rubenstein and Abbot, 2017). Habitat specialist fishes on the other hand provide a unique opportunity to study social evolution as they often reside in groups with low relatedness due to a pelagic larval phase (contrary to most terrestrial species; Avise and Shapiro, 1986; Buston et al., 2007; but see Buston et al., 2009). In particular, coral gobies of the genus *Gobiodon* are ideal for testing hypotheses about sociality as they display a wide variety of social phenotypes (Thompson et al., 2007; Wong et al., 2007), are easily observed because they occupy discrete habitat patches (Wong and Buston, 2013) and their phylogenetic relationships are reasonably well established (Duchene et al., 2013; Hing et al., 2017).

Several previous studies have examined phylogenetic relationships among species of *Gobiodon* (Agorreta et al., 2013; Duchene et al., 2013; Harold et al., 2008; Herler et al., 2009; Thacker and Roje, 2011). However, these studies have focused on relationships within the genus or more broadly at the family level (Gobiidae). To date, no studies have investigated the phylogenetic patterns of sociality in this genus. Duchene et al. (2013) examined the coevolution of *Gobiodon* species with their host corals and provides the most recent and comprehensive phylogeny of the *Gobiodon* genus. Likewise, there have been a number of studies investigating the causes and consequences of sociality in coral gobies (*Gobiodon* and *Paragobiodon*), but these studies have often focussed on a single species or a subset of species within the genus (Hing et al., 2018; Hobbs and Munday, 2004; Hobbs et al., 2004; Munday et al., 2006; Thompson et al., 2007; Wong, 2010, 2011; Wong et al., 2007). Furthermore, no studies so far have examined the relationship between sociality and ecological and life history traits across the genus *Gobiodon* while controlling for phylogeny, and hence tested key hypotheses of social evolution.

In this study we resolved the phylogenetic relationships within the genus *Gobiodon* at Lizard Island (Great Barrier Reef, Queensland, Australia) using seven molecular markers. Our reconstruction builds on the inferred phylogeny of Duchene et al. (2013) by increasing the number of molecular markers used, thereby inferring a phylogenetic tree with greater confidence. We then assessed the phylogenetic signal of sociality in the genus. Given previous work on *Gobiodon* demonstrated plasticity in social organization in response to extreme weather events (Hing et al., 2018), we expected to find a relatively weak phylogenetic signal of sociality. However, we did not know *a priori* what the strength of the signal would be and hence the extent to which shared evolutionary history of species would contribute to present day patterns of sociality. We therefore tested a range of ecological and life-history characteristics with phylogenetic structure in the models to assess the role these factors might have played in the evolution of sociality in *Gobiodon*.

Previous studies have shown significant relationships between group size and the factors of habitat size and body size in closely related species of coral gobies and more broadly in other species of habitat specialist fish (*Amphiprion percula*, Buston, 2003; *Paragobiodon*, *Gobiodon* and *Eviota*, Thompson et al., 2007; *Paragobiodon xanthosoma*, Wong, 2011). Most of the species in these previous studies form size based social hierarchies and habitat size and body size have been shown to predict group size in these species. A similar relationship has also been demonstrated between sociality and ecological generalism in

snapping shrimp (Brooks et al., 2017). Coral gobies are generally considered to be highly specialized in their choice of corals (Munday et al., 1997). However, we observed considerable variation in coral choice for some species, especially after extreme weather events (Hing et al., 2018). We also observed some variation in social structure and therefore aimed to investigate whether a relationship existed between sociality and host generalization. Hence, we specifically focused on two ecological variables: (i) host-coral size and (ii) host coral generalization (the ability to inhabit a broad range of host coral species), and one life-history variable (iii) body size, and assessed their relationship with sociality.

Finally, we present findings on *Gobiodon spilophthalmus* concerning its phylogenetic placement, which arose during our analyses. This is the first study to assess the phylogenetic basis and ecological and life history correlates of sociality in *Gobiodon* and therefore provides an important starting point for understanding the evolution of sociality in marine fishes.

## 2. Methods

### 2.1. Ethics approvals and research permits

All research activities for this study were conducted with the approval of the University of Wollongong Animal Ethics Committee (AE14-04, AE14-29). We conducted our research in the Great Barrier Reef Marine Park under permits G13/36197.1 and G15/37533.1.

### 2.2. Field sampling

Tissue samples of fifteen species of *Gobiodon* were collected from 23 sites around Lizard Island between February - March 2014 and January - February 2016 (Table 1, Fig. 1). However, *G. spilophthalmus* was removed from the analyses as barcoding analysis of the CO1 gene demonstrated the individuals collected were likely juvenile specimens of *G. acicularis* and *G. ceramensis* (Section 3.4). We searched all species of *Acropora*, *Stylophora*, *Seriatopora* and *Echinopora* known to host *Gobiodon* fishes along 30 m transects in the study area (Munday et al., 1999).

**Table 1**

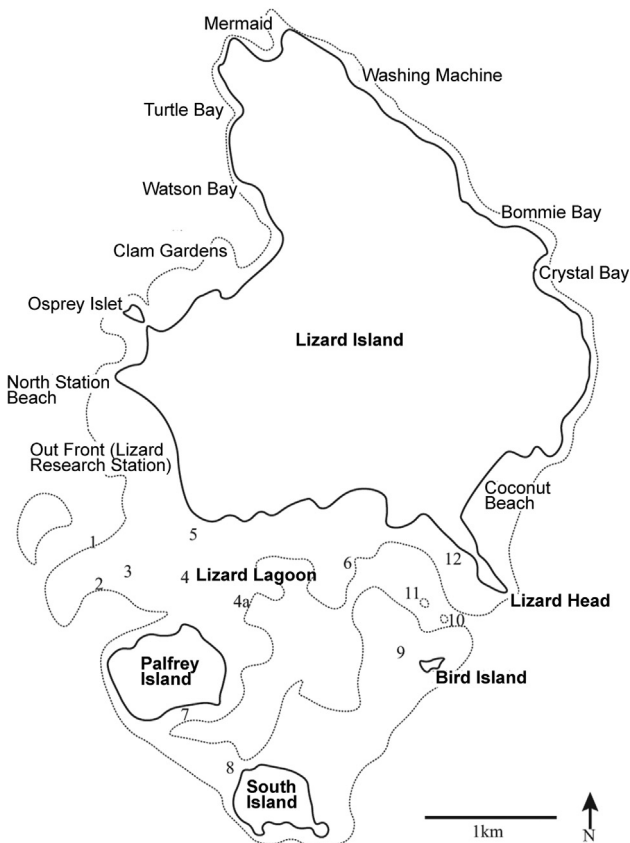
Goby species observed at Lizard Island with number of tissue samples obtained. Number of host-coral species was used as a measure of host-generalization. Mean standard length (SL) and host-coral size (CS) were calculated for each species.

Goby spp	Tissue Samples (n)	Coral species inhabited (n)	Mean SL (cm)	Mean CS (cm)
<i>G. acicularis</i>	3	1	1.91	55.20
<i>G. aoyagii</i> <sup>†</sup>	3	2	2.49	26.41
<i>G. axillaris</i>	3	4	3.09	23.76
<i>G. brochus</i>	4	9	2.54	16.50
<i>G. ceramensis</i>	6	2	2.69	27.23
<i>G. citrinus</i>	3	3	2.79	91.49
<i>G. erythropsilus</i>	3	11	2.60	23.31
<i>G. fuscioruber</i> <sup>††</sup>	4	10	2.75	29.95
<i>G. histrio</i>	3	10	2.80	23.22
<i>G. oculolineatus</i>	3	9	2.44	23.86
<i>G. okinawae</i>	3	11	2.12	43.95
<i>G. quinquestrigatus</i>	6	11	2.49	21.33
<i>G. rivulatus</i>	3	8	1.65	21.70
<i>G. spilophthalmus</i> c.f.*	6	–	–	–
<i>G. species D</i>	3	1	2.84	27.33
<i>P. xanthosoma</i>	1	1	1.72	26.53

<sup>†</sup> *G. aoyagii* was previously referred to as *G. species A* as a placeholder but has now been formally described by Shibukawa et al. (2013).

<sup>††</sup> *G. unicolor* (sensu Munday et al., 1999) was reassigned as *G. fuscioruber* by Herler et al. (2013).

\* Measurements of ecological and life-history factors were not obtained for *G. spilophthalmus* c.f. as they were determined to be juveniles of other species and excluded from analyses.



**Fig 1.** Map of study sites at Lizard Island, Australia. Dotted lines indicate reef structure. Site names are in regular font. Numbered sites are: Big Vickey's Reef (1); Vickey's Reef (2); Horse Shoe Reef (3); Palfrey Reef (4 – 4a); Loomis Reef (5); Trawler (6); Picnic Beach (7); Ghost Beach (8); Bird Island Reef (9); Entrance Bommie (10); Bird Bommie (11); Lizard Head Reef (12).

Transects were placed haphazardly at each site and only used as a reference to aid in the relocation of tagged corals (i.e. transects were not used for any kind of spatial analysis). In total, 21 species of coral were recorded.

Corals were searched by divers with the aid of an underwater light for the presence of gobies. Corals hosting gobies were identified to species and measured along three axes (length, width and height: Hing et al., 2018). Gobies were removed from the corals by anaesthetising them with a clove oil solution and creating a current by hand (Munday and Wilson, 1997). The species and number (group size) of captured fish was recorded and brought to a boat for processing. On the boat, fish were placed into a large container of regularly refreshed seawater to maintain constant temperature and aeration. Each fish was anaesthetised and measured to the nearest 0.01 cm with vernier callipers and a small caudal fin clip (~1–2 mm) of each individual was preserved in ethanol. After processing, fish were released back to their original coral of capture.

### 2.3. Ecological and life-history factors

Coral size was calculated as the simple average diameter,  $(L + W + H)/3$  as it provides a good representation of the major axis of the coral (Kuwamura et al., 1994). Ecological generalisation was assessed as the number of host-coral species each goby species was observed to occupy. We added observations from three subsequent field trips between August 2014 and February 2016 for the ecological generalisation analyses as two cyclones impacted the study site over this period (Hing et al., 2018). We reasoned that these impacts had the potential to alter normal patterns of residency and species adhering to a

'specialist' strategy would possibly broaden their host-species range under extreme circumstances. We therefore wished to capture any variation these disturbances caused for this analysis.

Body size was chosen as a life-history trait of interest for this study. We measured the standard length (tip of the snout to caudal peduncle) of each individual. Standard length was used rather than total length as many individuals had sustained damage to the caudal fin and an accurate measure of total length could not be obtained.

### 2.4. Sociality index

We used a sociality index proposed by Avilés and Harwood (2012). The index is an average for each species, of the proportion of groups in the study population, proportion of subordinates in the study population and proportion of the life-cycle spent in a group. The proportion of the life-cycle spent in a group may be an important indicator of delayed dispersal in some species. However, coral gobies undergo a pelagic larval phase prior to joining a group where they typically remain in a social queue to obtain breeding status (i.e. they do not delay dispersal, but do tend to remain in a group once settled). Therefore, we assumed the proportion of the life-cycle spent in the group was 1 for all species and the main variation in sociality in coral gobies was caused by the remaining two components of the sociality index. The proportion of groups in the study population is indicative of a species' tendency to form groups, while the proportion of subordinates in the study population (associated with the proportion of groups) is an indication of behaviour in terms of the subordinate's willingness to join a group and the dominant member's willingness to tolerate them. The social index ranges from 0 to 1. Raw index values were used in the Generalized Least Squares analyses (Section 2.9).

### 2.5. DNA extraction, amplification and sequencing

DNA was extracted from fin clips for two to three individuals of each species of *Gobiodon* and one individual *Paragobiodon xanthosoma* which was used as an outgroup to the *Gobiodon* genus (Table 1). We used a standard Proteinase-K salting out procedure to extract DNA (Aljanabi and Martinez, 1997). DNA was resuspended in 20–50 µl of TE solution (1 mM Tris-HCl, 0.1 mM ethylenediaminetetraacetic acid [pH 8]) and stored at 4 °C. We amplified nuclear recombination activating gene 1 (RAG1), nuclear zinc finger protein of the cerebellum 1 (ZIC1) and the mitochondrial cytochrome c oxidase subunit 1 (CO1) gene using generic fish primers for each gene (primer sequences available in Supplementary Table S1; Holcroft, 2005; Li et al., 2007; Ward et al., 2005 respectively). Where weak amplification occurred, goby specific primers were designed using an alignment of the appropriate gene region made up of sequences obtained from species which showed strong amplification (Supplementary Table S1). Polymerase Chain Reactions (PCRs) were performed using MyTaq Polymerase (Bioline, Australia) in accordance with the manufacturer's instructions. The PCR conditions consisted of 2 min at 95 °C, 35 cycles of 1 min at 94 °C, 1 min at 45–65 °C (optimised for each gene and species), 1 min at 72 °C and a final elongation of 5 min at 72 °C. PCR products were checked for length and strength of amplification using 1% agarose gel electrophoresis. ExoSAP-IT (GE Healthcare, Bucks, UK) was used to treat each PCR product prior to sequencing using the ABIPRISM BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems, Australia). Each PCR product was sequenced in both the forward and reverse direction.

### 2.6. Sequence alignment

Alignment of RAG1, ZIC1 and CO1 genes was trivial, because there were no internal indels in the alignment – both ClustalW and MUSCLE (within MEGA7; Kumar et al., 2016) produced alignments with only leading and trailing gaps, where the length of reliable sequence was slightly different. The default settings for both ClustalW and MUSCLE



were used.

Once COI, RAG1 and ZIC1 sequences had been obtained for 2 to 3 individuals of each species, consensus sequences were established using Bioedit (Hall, 1999). We then constructed additional consensus sequences for 12S and 16S rRNA genes (obtained from GenBank, accession numbers available in [Supplementary Table S2](#)) for the species in our study and obtained further consensus sequences for the nuclear ribosomal protein S7 Intron 1 chromosome 2 (S7I1) gene and mitochondrial cytochrome b (cytb) from GenBank ([Supplementary Table S2](#); Duchene et al., 2013; Harold et al., 2008; Herler et al., 2009). All seven genes (RAG1, ZIC1, S7I1, COI, cytochrome b, 12S and 16S) were concatenated for each species.

## 2.7. Phylogenetic analysis

Partitioning schemes and nucleotide substitution models were established with PartitionFinder version 1.1.1 (Lanfear et al., 2012) using the corrected Akaike Information Criterion (AICc) and a heuristic search algorithm with branch lengths unlinked. We performed the analysis on 7 datablocks, one for each gene. Priors for the branching process and times were set as follows: the tree prior was a Yule model, the birth rate had a uniform prior, as did the clock rates for each of the gene partitions. A strict clock was set for each partition, but the clock rate was unlinked between partitions. Phylogenetic trees were then inferred from Bayesian analysis conducted on BEAST2 v2.4.2 (Bouckaert et al., 2014; Drummond et al., 2012) in which unlinked partitions and a Markov Chain Monte Carlo (MCMC) process with a chain length of 100 million was specified. No calibration information was used as we only wished to examine relative estimates of branching times. Separate BEAST analyses were also conducted on the concatenated mitochondrial data (since the mitochondrial genes represent a single, linked locus), and each nuclear gene fragment. These trees are reported in the [supplementary material](#). The trees recovered from the individual nuclear gene analyses were generally poorly resolved, with many nodes having low posterior probability support. This is not surprising given the relatively small size of these datasets. The mitochondrial tree was well resolved (with high posterior probability support), but differed in the placement of one clade (i.e. [Fig. 3](#), clade B) when compared with the ‘full data’ set. We focus here on the ‘full data’ set, because it is larger and contains information from multiple (mitochondrial and nuclear) sources.

Stationarity was assessed with Tracer v1.6 (Rambaut et al., 2018). In initial BEAST analyses, stationarity was not reached after 100 million generations (expected sample sizes (ESS) values generally less than 200), primarily because some parameter values were very close to zero. However, when the nucleotide substitution model for 6 of the 7 gene partitions was simplified (from GTR to HKY; in one of the gene partitions, PartitionFinder suggested JC69, and this was kept as JC69), stationarity was reached after 100 million generations, with all ESS values greater than 200. A maximum likelihood analysis was also conducted using “Randomized Accelerated Maximum Likelihood” (RAxML) version 8 (Stamatakis, 2014). The Gamma model of rate heterogeneity was used with branch lengths optimized per gene and the proportion of invariable sites estimated. A maximum likelihood search was then applied to find the best scoring tree.

## 2.8. Phylogenetic signal

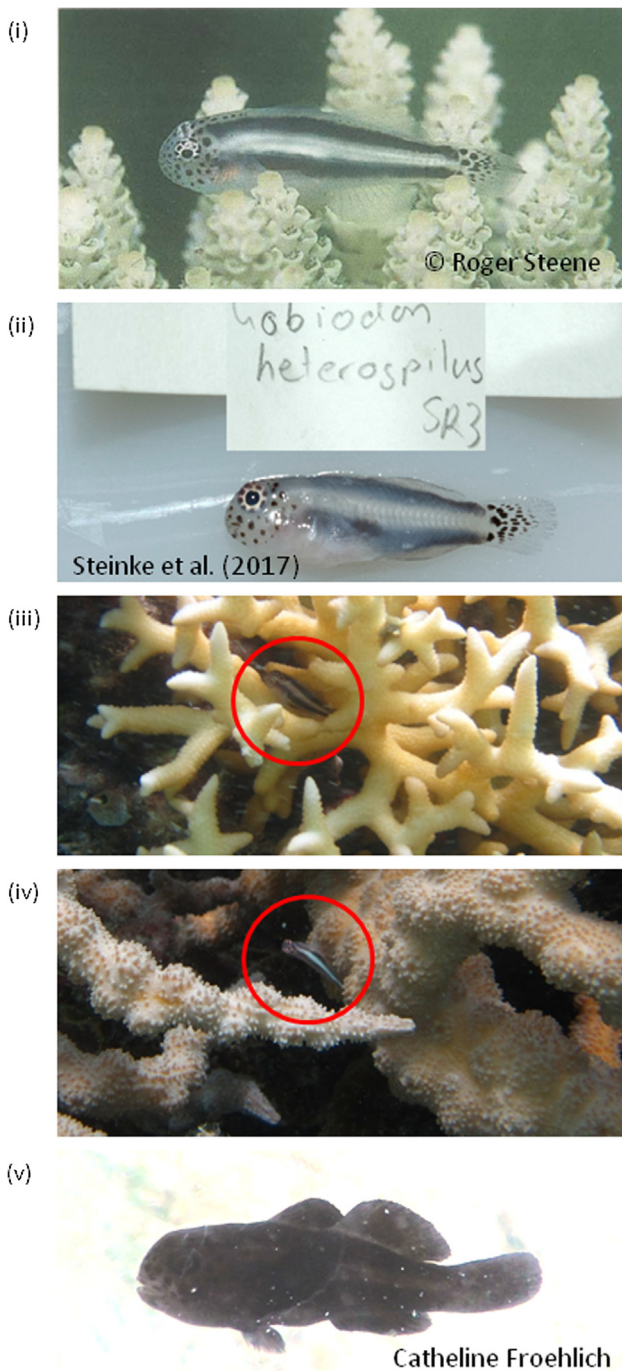
Phylogenetic signal of sociality was calculated in R using the `phyloSig()` function of the `phytools` package (Revell, 2012). We used the social index for each species and the Bayesian summary tree for the analyses. We calculated both Pagel’s lambda (Pagel, 1999) and Blomberg’s K (Blomberg et al., 2003) statistics and produced tests against a null hypothesis of no phylogenetic signal using a likelihood ratio test and randomization test respectively.

## 2.9. Phylogenetic generalized least squares models

Phylogenetic Generalized Least Squares was used to assess relationships between sociality and ecological and life-history traits while taking into account phylogenetic non-independence between species. Sociality index was the dependent variable and the ecological and life-history traits were included as main and interacting effects. We used a summary of the Bayesian inferred phylogenetic tree for this analysis. All pGLS analyses were conducted using the `nlme` package in R (Pinheiro et al., 2018). Four models of trait evolution (Brownian motion, Pagel’s Lambda, Blomberg ACDC and Ornstein-Uhlenbeck) available in the `ape` package (Paradis et al., 2004) were applied to each of the relationships. As we had no *a priori* expectations of the type of selection sociality might be under, we chose the best model to present by comparing Akaike’s Information Criterion (AIC). An analysis of deviance was conducted using the `Car` package (Fox and Weisberg, 2011) on the best model to identify factors that significantly deviated from the null model.

## 2.10. *Gobiodon spilophthalmus*

*Gobiodon spilophthalmus* was first described by Fowler (1944). However this description was based upon a single preserved specimen. We therefore based our identification on Munday et al. (1999) who provide a live specimen photo and describe *G. spilophthalmus* as uniform black in colour and only distinguishable from *G. ceramensis* (also uniform black as adults) in the juvenile phase. The juveniles of *G. spilophthalmus* are white with black stripes along the body and black spots on the head ([Fig. 2\(i\)](#)). We collected specimens morphologically similar to those depicted in Munday et al. (1999) as *G. spilophthalmus*. During collection, we noted a small *G. ceramensis* changed colour upon capture from uniform black to the black and white stripes and spots similar to that described for juvenile *G. spilophthalmus*. This was observed again in 2019 by colleagues at One Tree Island, Australia (Froehlich pers. comm.; [Fig. 2\(v\)](#)). These observations prompted a closer examination of our *G. spilophthalmus* c.f. specimens. *G. spilophthalmus* c.f. specimens were found on the coral species *Seriatopora hystrix* and *Echionopora horrida* which are also inhabited (almost exclusively) by *G. ceramensis* and *G. acicularis* respectively ([Fig. 2\(iii, iv\)](#) photos). Other *G. spilophthalmus* c.f. specimens were sometimes observed associating with groups of *G. ceramensis* or *G. acicularis*. To investigate this further, we sequenced the barcoding region (COI) of individuals resembling *G. spilophthalmus* from independent colonies of *S. hystrix* and *E. horrida*, and compared them with individuals of *G. ceramensis* and *G. acicularis*. First, we conducted an Automatic Barcode Gap Discovery (ABGD) analysis which groups COI sequences into hypothetical species based on automatic detection of the ‘barcode gap’, the natural break in sequence divergence that occurs when within-species divergence is compared to between-species sequence divergence (Puillandre et al., 2012). We used the default settings and Kimura 2-P (K80) distances. We then conducted a Bayesian phylogenetic analysis of the COI gene of *G. acicularis*, *G. ceramensis* and *G. spilophthalmus* c.f. using BEAST2. In this analysis we coded each individual with the species of coral it was collected from. We used the same methods described above (Sections 2.6 and 2.7) for sequence alignment and Bayesian analysis to infer a gene tree for this species group using *G. okinawae* as an outgroup. Furthermore, *Gobiodon heterospilos* is described as similar in appearance to *G. spilophthalmus* but lacking the black body stripes (presumably in the juvenile phase; Munday et al., 1999). Steinke et al. (2017) deposited three COI sequences on the BOLD database for *G. heterospilos* from Lizard Island, however the photo attached to the only juvenile in their collection (BOLD record LIF847-08) clearly possesses black body stripes. We therefore conducted a second Bayesian phylogenetic analysis using the same methods described above (sections 2.6 and 2.7) of our specimens of *G. acicularis*, *G. ceramensis*, *G. spilophthalmus* c.f. and the *G. heterospilos* sequences deposited by Steinke et al. (2017) in order to determine



**Fig 2.** *Gobiodon spilophthalmus* as depicted by Munday et al. (1999)(i) and *G. heterospilos* sample deposited by Steinke et al. (2017) on the BOLD database, record LIFS847-08 (ii). Specimens from our collection matching descriptions of juvenile *G. spilophthalmus* collected in 2014 from *Seriatopora hystrix* (iii) and *Echinopora horrida* (iv). A small *G. ceramensis* transitioning from the suspected juvenile spots and stripes pattern to the uniform black adult phase (v).

if *G. heterospilos* c.f. could be differentiated from species identified in our collection.

### 3. Results

Our results suggest a combination of ecological and life-history factors contributed to the evolution of sociality in the *Gobiodon* genus, but sociality by itself also has some evidence of a phylogenetic signal. Phylogenetic analyses by two methods inferred identical species

composition of four clades giving high confidence in the phylogenetic tree used for pGLS analyses. Phylogenetic generalized least squares analyses then demonstrated coral size and mean body size of the species likely have a strong influence on the extant social state of a species (Section 3.3).

#### 3.1. Phylogenetic inference

Both analyses; Bayesian and maximum likelihood, produced four clades (A-D; Fig. 3) containing exactly the same *Gobiodon* species within each clade. The main difference between both analyses was the Bayesian tree inferred 2 main sister groups (A/B and C/D sister clades) with strong support (posterior probability 1.00) while the maximum likelihood tree was unresolved at the base of each sister clade (bootstrap support < 50). However it still produced the same 4 clades with the same configuration. The two main sister groups inferred with the Bayesian tree each in turn formed two sister clades: clade A and B with moderate support (posterior probability 0.79) and the sister clades of C and D with strong support (posterior probability 0.99). Clade A resolved *G. acicularis* and *G. ceramensis* as sister species (posterior probability 1.00), and contained two other species, *G. okinawae* (posterior probability 1.00) and *G. citrinus* (posterior probability 1.00) (Fig. 3). The species *G. oculolineatus*, *G. quinquestrigatus*, *G. species D* and *G. rivulatus* made up clade B with *G. quinquestrigatus* and *G. species D* as sister taxa (posterior probability 1.00) (Fig. 3). Clade C contained a single sister species group made up of *G. aoyagii* and *G. brochus* (posterior probability 0.99) (Fig. 3). Clade D contained two sister species groups, the first consisting of *G. histrio* and *G. erythrosphilus* (posterior probability 1.00) and the second consisting of *G. fuscus* and *G. axillaris* (posterior probability 1.00) (Fig. 3).

In the maximum likelihood analysis, the node giving rise to the A/B/C group could not be resolved with any certainty (bootstrap support < 50). However the configuration of the species within each clade was identical to the Bayesian analysis and resolved with moderate to strong bootstrap support (75 – 100). The strong support for the nodes within each clade in both analyses signifies reasonable confidence in the species composition of each clade. The Bayesian analysis produced a tree with very high posterior probabilities (with the exception of the node relating clades A and B). We therefore based all further analyses on the Bayesian analysis.

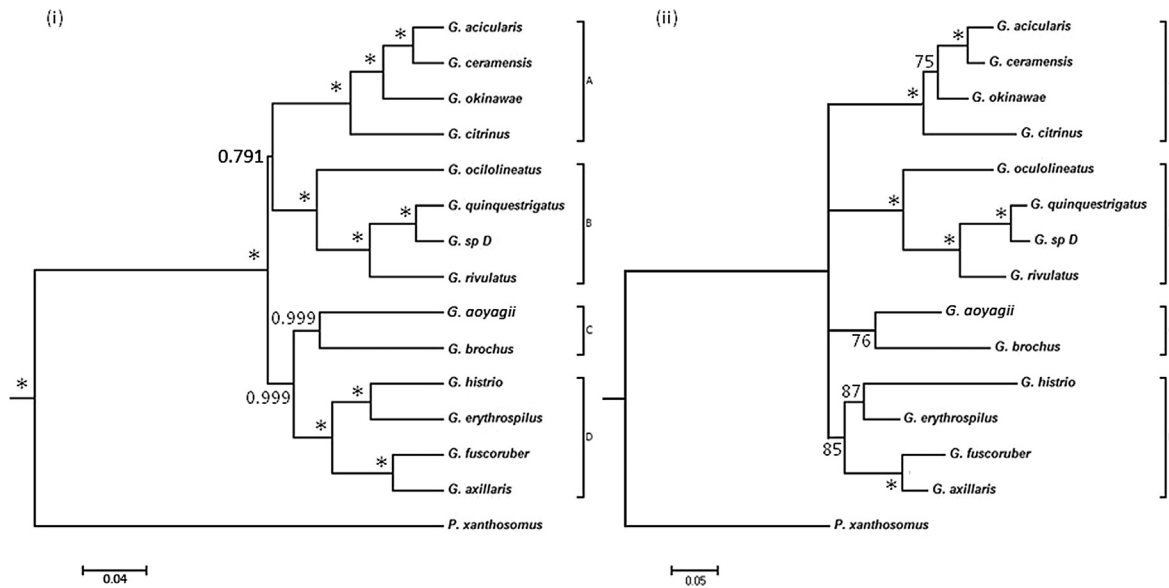
#### 3.2. Phylogenetic signal

There was some evidence of a phylogenetic signal of sociality in the *Gobiodon* genus. We found little evidence of a phylogenetic signal of sociality in the genus using Pagel's lambda ( $\lambda = 0.614$ ,  $P = 0.349$ ). However, Blomberg's *K* displayed some evidence of a phylogenetic signal of sociality ( $K = 0.802$ ,  $P = 0.035$ ). Although the value of *K* represents a relatively low signal, the significant test result indicates it was stronger than expected under a random distribution of the trait (sociality).

#### 3.3. Phylogenetic generalized least squares

There was a significant interaction between coral size and mean fish length in the pGLS model predicting sociality (analysis of deviance,  $df = 1$ ,  $\chi^2 = 4.845$ ,  $\lambda = 1.043$ ,  $P = 0.028$ ). The model predicted coral size would have little impact on sociality for smaller species, but smaller species would generally be more social (social index approximately 0.75, Fig. 4). On the other hand, sociality in larger species was much more dependent on host-coral size (Fig. 4). In other words, smaller species overall are predicted to be more social than larger species regardless of the size of coral they inhabit, whereas larger species are predicted to exhibit sociality only when corals are large.

There were no significant interactions between coral size and host generalization or mean fish-length and host generalization on sociality



**Fig 3.** Phylogeny of *Gobiodon* present at Lizard Island based on 7 molecular markers (4 mtDNA; COI, cytb, 12S, 16S and 3 nuclear DNA; RAG1, ZIC1, S711) produced with Bayesian (i) and maximum likelihood (ii) methods. Node values in (i) are posterior probability where \* indicates a value of 1. Node values in (ii) are bootstrap percentages where \* indicates a value of 100.

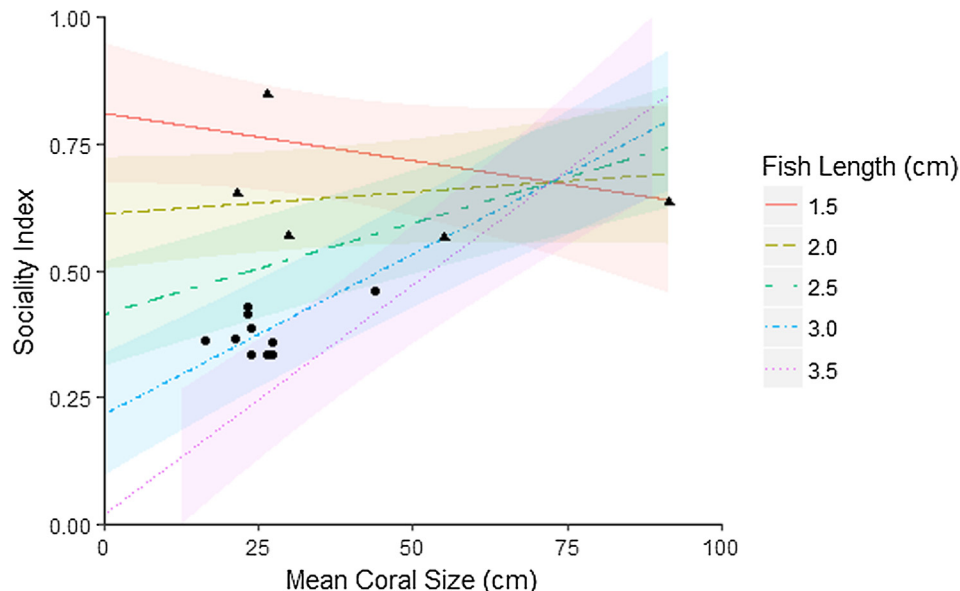
in the respective models ( $df = 1$ ,  $\chi^2 = 0.781$ ,  $\lambda = 1.073$ ,  $P = 0.377$ ;  $df = 1$ ,  $\chi^2 = 0.024$ ,  $\lambda = 1.073$ ,  $P = 0.878$  respectively, Fig. 5). This means there was no significant difference in the relationship between sociality and host-coral size between species that adhere to either specialist or generalist host strategies. Likewise, there was no significant difference in the relationship between sociality and fish-length between host-specialist and -generalist species. The main effect of host generalization alone was also non-significant ( $df = 1$ ,  $\chi^2 = 0.063$ ,  $P = 0.803$ ) indicating that the ability to occupy a greater host-range is not likely to facilitate sociality in these species.

While the detection of a phylogenetic signal of sociality was somewhat unconvincing in the test of Pagel's Lambda and Blomberg's  $K$  (Section 3.2), the pGLS analyses showed a strong indication of phylogenetic signal ( $\lambda > 1$ ). Taken together these results indicate there is some phylogenetic signal of sociality, but other effects (such as ecology and life-history) are probably equally, if not more important in

determining the extant social state of a species.

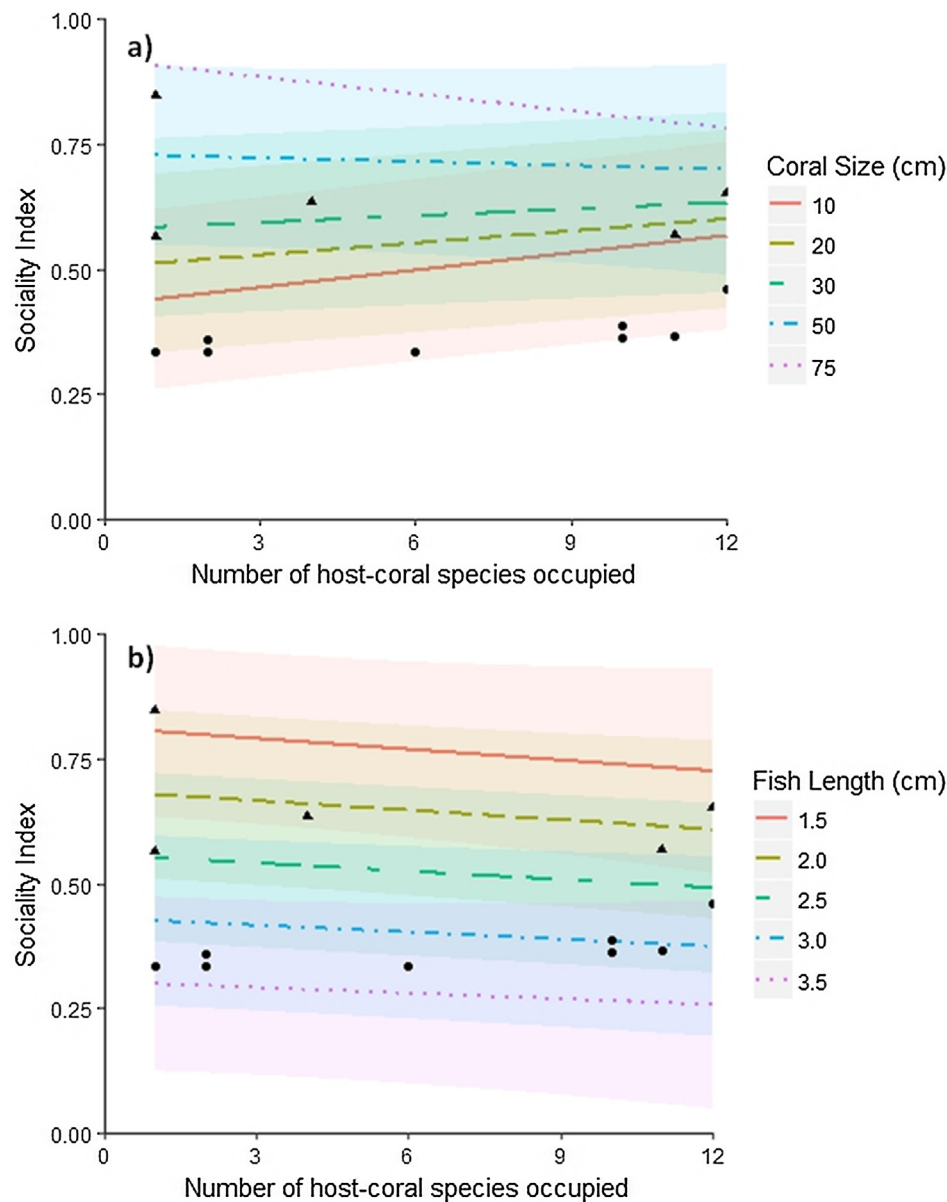
### 3.4. *Gobiodon spilophthalmus*

Our analyses revealed the *G. spilophthalmus* c.f. specimens were likely juveniles of *G. acicularis* or *G. ceramensis* depending on which coral species they were collected from. The ABGD analysis revealed two distinct species groups, with the *G. spilophthalmus* c.f. specimens collected from *S. hystrix* grouping with *G. ceramensis* and those collected from *E. horrida* grouping with *G. acicularis*. This pattern was also supported in the Bayesian analysis of these COI sequences (Fig. 6). This phylogeny showed *G. spilophthalmus* c.f. grouping with both *G. ceramensis* and *G. acicularis*, depending on their respective host corals. *Gobiodon ceramensis* did split into two groups in this analysis, but HKY distances ranged from 0.2% to 0.7% indicating extremely low divergence in the COI sequences, a strong indication they should be



**Fig 4.** Model predictions for the interacting effects of host-coral size and fish length on sociality index. Raw data are pair-forming species (circles) and group-forming species (triangles). Modelled species sizes, indicated by different line types (figure legend), range from 1.5 cm (solid) to 3.5 cm (dotted).





**Fig 5.** Interacting effects of mean coral size and host-generalization (a) and mean fish length and host-generalization (b) on sociality. Lines in a) are different average coral sizes from 10 cm (solid line) to 75 cm (dotted line). Lines in b) are different mean fish length from 1.5 cm (solid line) to 3.5 cm (dotted line). Both (a) and (b) raw data are individual species conforming to group-forming (triangles) or pair-forming (circles) strategies.

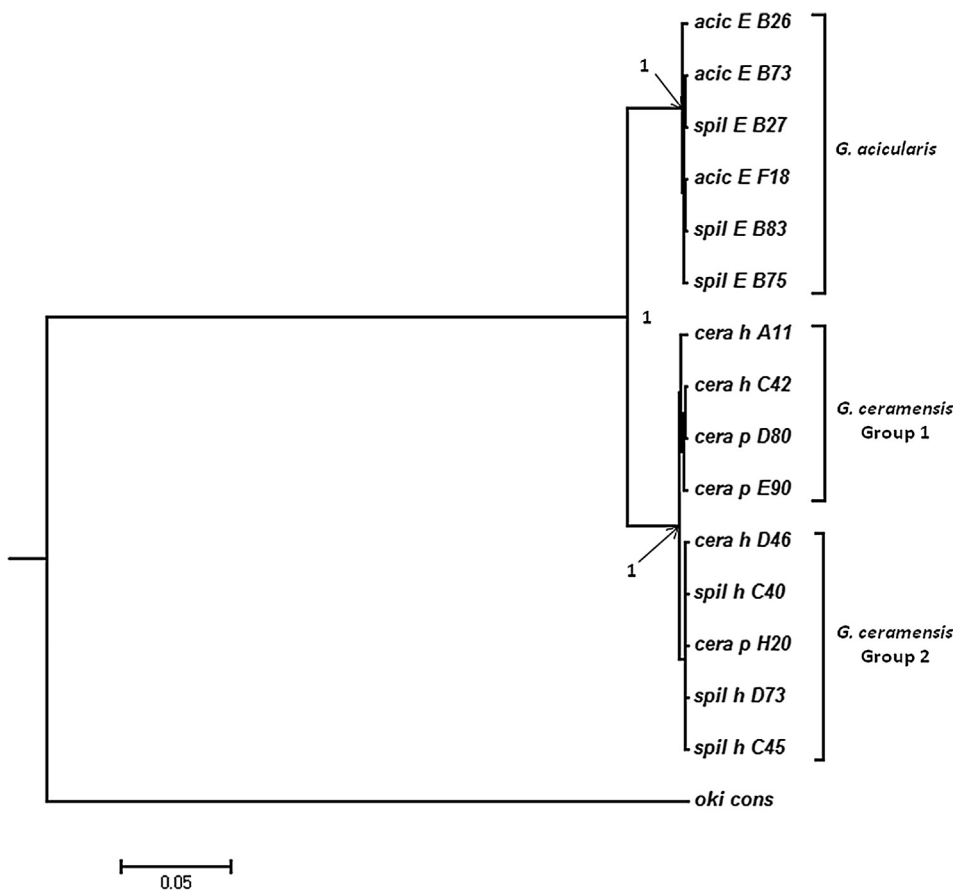
considered a single species. When we included the *G. heterospilos* sequences deposited by [Steinke et al. \(2017\)](#) into a Bayesian phylogenetic analysis with our *G. spilophthalmus* c.f., *G. ceramensis* and *G. acicularis* specimens, the *G. heterospilos* samples were placed in the same groups as *G. spilophthalmus* c.f. (collected from *S. hystrix*) and *G. ceramensis* (posterior probability 0.999). We therefore suspect [Steinke et al. \(2017\)](#) understandably misidentified these specimens in their study and we did not include them in further analyses. These analyses indicate the specimens we collected, which were morphologically similar to *G. spilophthalmus*, were most likely juveniles of either *G. ceramensis* or *G. acicularis* and could be reliably differentiated by the species of coral they were collected from. We therefore did not include *G. spilophthalmus* in our broader phylogenetic analyses.

#### 4. Discussion

Our analyses provide evidence of some phylogenetic signal of sociality in the coral-gobies, *Gobiodon*. In contrast to several other

vertebrate groups which display strong phylogenetic signals of sociality, our findings suggest factors such as ecology, life-history or both, likely have a stronger impact on which species display sociality at any given time ([Kruckenhauser et al., 1999](#); [Nowicki et al., 2018](#); [Shultz et al., 2011](#)). In support of this, [Hing et al. \(2018\)](#) showed the mean group size of social species of *Gobiodon* displayed plastic responses following multiple major ecological disturbances, suggesting sociality may be quite flexible in *Gobiodon* species rather than phylogenetically constrained.

While [Hing et al. \(2018\)](#) did not delve into any species-specific trends, it is possible the observed social plasticity was driven by a few key species (e.g. *G. acicularis*, *G. erythrospilus*, *G. fuscioruber*, *G. histrio* and *G. okinawae*). These particular species have social indices close to 0.5 (the value exactly half-way between theoretically perfect sociality and completely solitary) because there was a relatively even proportion of groups and pairs in the study population ([Hing et al., 2018](#)). This indicates a certain level of social plasticity in these species – when conditions allow, they will form groups, but they are also able to



**Fig 6.** Phylogenetic tree produced with Bayesian analysis showing *G. acicularis* grouping with specimens resembling *G. spilophthalmus*, and the two groups of *G. ceramensis* also recovered with specimens resembling *G. spilophthalmus*. Node values are posterior probabilities. Values for internal nodes of each species group are not displayed as the placement of individuals within each group is irrelevant. Species names are abbreviated to acic (*G. acicularis*), spil (*G. spilophthalmus* c.f.), cera (*G. ceramensis*) and the outgroup, oki (*G. okinawae*). Letters immediately following each species abbreviation indicates the coral species the specimen was collected from; *Echinopora horrida* (E), *Seriatopora hystrix* (h) and *Stylophora pistillata* (p). The last three characters are an individual identifier. The outgroup was a consensus sequence (cons) of the COI gene.

survive as a breeding pair. These species are therefore prime candidates for further study of social plasticity.

Like many cryptobenthic fishes, *Gobiodon* species have a pelagic larval phase where the larvae are mixed with other nektonic organisms (Brandl et al., 2018). It therefore seems likely that relatedness within the group would be low, as for other marine fishes (Avisé and Shapiro, 1986; Buston et al., 2007; but see Buston et al., 2009), although this is yet to be empirically tested. Low relatedness reduces the value of 'r' in Hamilton's rule and hence the likelihood of sociality evolving, all else being equal (Bourke, 2014; Hamilton, 1964). For sociality to evolve in such groups, there must therefore be other factors which alter the direct costs and benefits of group living. This was recently demonstrated in freshwater cichlids by Dey et al. (2017) who found direct benefits provided from group living, biparental care and diet type, were more influential than relatedness (associated with social monogamy) in the evolution of cooperative breeding, a complex form of sociality. This contrasts with many other vertebrate lineages which often form groups of closely related individuals and in which indirect (kin) benefits are likely to have heavily influenced the evolution of social groups (Bourke, 2014; Halliwell et al., 2017; Lukas and Clutton-Brock, 2012; While et al., 2009; but see Riehl, 2013). This emphasis on direct costs and benefits represents an alternate pathway to complex sociality to the kinship-based pathway often proposed in the vertebrate literature. Alternatives such as this are worthy of further exploration as they offer novel insights into the evolution of sociality (Dey et al., 2017; Riehl, 2013).

We tested factors known to provide direct fitness benefits in other closely related species, namely the effects of host coral size, host coral generalization (ecological factors) and body size (life-history factor) on sociality (Buston, 2003; Thompson et al., 2007; Wong, 2011). We found there was a significant interaction between host coral size and body size on the degree of sociality when phylogenetic correlation was accounted

for. The relationship between host coral size and sociality was stronger for larger species. This makes intuitive sense as individuals of larger species would presumably take up more physical space in a coral. Hence, for larger bodied species to form groups, they would need to inhabit larger corals on average. On the other hand, smaller species could potentially form larger groups in a much larger size-range of corals before the habitat becomes saturated and group members are forced to disperse from the group. Group sizes of various social fish species are not only influenced by habitat size, however, and are instead related to size differences maintained between adjacent ranked individuals (Mitchell and Dill, 2005; Buston et al., 2007; Ang and Manica, 2010; Wong 2011). Thus, it is also possible that smaller bodied species of *Gobiodon* maintain larger size ratios (smaller size differences) between adjacent ranked group members than larger bodied species, which would be an important avenue of future research.

Although smaller species showed less of a relationship between sociality and host-coral size, they were more social overall than larger species. This may indicate that smaller species obtain greater direct fitness benefits from social living or face greater constraints of dispersal or greater costs of solitary living. For example, smaller species might be more prone to predation or less competitive for vacant habitat compared to larger species, thus limiting dispersal opportunities and enhancing the benefits of remaining within a group (Helfman and Winkelman, 1997; Munday and Jones, 1998). This finding is again at odds with other terrestrial vertebrate systems which generally exhibit a positive relationship between sociality and body size (Armitage, 1981; Bekoff et al., 1981). This discrepancy between terrestrial and marine vertebrates highlights the importance of studying animal groups with varying life-history strategies.

While host generalization has been proposed as a driver of sociality in some habitat specialist marine species (Brooks et al., 2017), we found no evidence that it played a role in *Gobiodon* sociality. There was



considerable variation in the number of host-coral species inhabited by each species of *Gobiodon* but this variation showed no discernable pattern in association with sociality. Munday et al. (1997) demonstrated *Gobiodon* species have distinct coral preferences. However, our research suggests some species appear to be more capable of relaxing this preference than others (especially during intense ecological disturbance; e.g. Hing et al., 2018). This ability does not however, appear to be related to sociality. The coral preferences displayed by many *Gobiodon* species may be due to properties of particular coral species such as complexity, branch length or inter-branch distances (Untersteeggaber et al., 2014). Sociality might therefore be influenced by coral properties, not measured in this study rather than variation in host-preference. For example more complex corals might increase the benefits of remaining in the group (for example by offering greater protection from predators) and thereby promote sociality. A similar pattern of increasingly complex habitat and a higher density of lizard aggregations has been documented by Michael et al. (2010). Untersteeggaber et al. (2014) demonstrated that coral occupancy by *G. histrio* and *G. rivulatus* was related to coral size and branch length. Given our findings on sociality and coral size, coral architecture would be an interesting factor to consider in future studies of *Gobiodon* sociality.

To date, there have been few comparative studies of marine fishes looking at phylogenetic, ecological and life-history correlates of sociality across multiple species (Hing et al., 2017; but see Nowicki et al., 2018). In contrast, numerous studies in other vertebrate systems have been instrumental in developing our current understanding of how ecology (Brown, 1974; Emlen, 1982; Kokko et al., 2002; Kokko and Ekman, 2002; Stacey and Ligon, 1991) and life-history (Arnold and Owens, 1998; Hatchwell and Komdeur, 2000; Rowley and Russell, 1990) have influenced the evolution of sociality in these systems (reviewed in Hing et al., 2017). For example, phylogenetic reconstructions of sociality in other vertebrate systems have revealed non-random clustering in birds and mammals (Arnold and Owens, 1998; Briga et al., 2012; Edwards and Naem, 1993). Closer examination at the genus level has revealed likely ecological and life-history correlates of sociality (e.g. Armitage, 1981; Faulkes et al., 1997). We have now added a comparatively understudied group of vertebrates with non-conventional life-histories (marine fishes) to this knowledge base. Unconventional life-history strategies (such as bi-directional sex change observed in several species of *Gobiodon*; Cole, 2011; Cole and Hoese, 2001; Munday et al., 1998; Nakashima et al., 1996) likely alter the costs and benefits of group living in these social systems and therefore represent a unique perspective on social evolution (Buston and Wong, 2014; Hing et al., 2017; Wong and Buston, 2013).

#### 4.1. Comparison of taxonomic structure

We built upon the phylogeny of Duchene et al. (2013) by adding additional molecular markers. Our Bayesian analysis inferred similar species composition (albeit with fewer species as we did not sample from the Red Sea) of each clade to that of Duchene et al. (2013), but the placement of the clades relative to each other varied between the two studies. Both studies inferred two sister species groups with high posterior probability. However, the sister clades C/D in our study, inferred with strong support, were not sister to each other in Duchene et al. (2013). Instead clade C was sister to clade A and the other group consisted of clades B/D in Duchene et al. (2013). Our tree provides very strong support for the sister group C/D while the node relating clades C and A in Duchene et al. (2013) is inferred with moderate support. However the A/B group in our study was not strongly supported. It seems there is broad agreement in the species composition of each clade. However, further research into the relationships between the clades is clearly required to discern the true genetic structure of the genus.

#### 4.2. *Gobiodon spilophthalmus*

We determined our *G. spilophthalmus* c.f. specimens were in fact juveniles of either *G. ceramensis* or *G. acicularis* depending on the host-coral they were collected from. To our knowledge this is the first record of these species having juveniles of similar appearance to each other and to those described as *G. spilophthalmus* (Fowler, 1944; Munday et al., 1999). Our findings raise several possibilities. First, *G. spilophthalmus* may not be a valid species. The phylogeny produced by Duchene et al. (2013) shows very low support for the node relating *G. spilophthalmus* to *G. ceramensis* indicating there was difficulty delineating these samples as separate species. Harold et al. (2008) recognise *G. spilophthalmus* as a valid species, but do not include it in their phylogeny of Indo-Pacific *Gobiodon* species. Second, *G. spilophthalmus* could be a valid species but is not present at Lizard Island. We cannot rule this possibility out with our data, but we find it unlikely that a species described from the New Hebrides (Vanuatu) would not be present at Lizard Island especially given the broad distribution of its congeners (Fowler, 1944; Munday et al., 1999). Additionally, Munday et al. (1999) describe *G. spilophthalmus* as occurring throughout the range of their collections which includes the Great Barrier Reef and Papua New Guinea. Third, *G. spilophthalmus* is a valid species and is present at Lizard Island, but we did not sample any. Although we sampled as many reefs as possible at Lizard Island, fourteen goby colonies may not be representative of the whole Lizard Island population, especially if *G. spilophthalmus* is rare. Additionally, there is clearly confusion around the identification of *G. heterospilos* and *G. spilophthalmus* in the literature (Fowler, 1944; Munday et al., 1999; Steinke et al., 2017), assuming both are indeed valid species as recognized by Harold et al. (2008).

Assuming *G. spilophthalmus* is a valid species, it appears to have diverged very recently and is therefore very closely related to its sister species, *G. ceramensis* (Duchene et al., 2013). It is likely the genetic markers used in our analysis (COI) and other studies featuring *G. spilophthalmus*, are evolving more slowly than this clade is speciating and thus not capable of fully capturing the true genetic structure of these species. The conflicting possibilities presented above and this issue of recent speciation outpacing divergence in the COI marker, highlight the need for a full genomic study of this clade to determine the validity of these species. Detailed ecological observations would also be highly desirable to establish field identification guidelines for each species, if indeed they can be reliably differentiated in the field.

#### 5. Conclusion

The phylogenetic signal of sociality in *Gobiodon* could not be conclusively resolved. However, we found a combination of life-history and ecological effects best predicted sociality in these species. Previous research suggests that sociality is probably quite plastic in *Gobiodon* and supports the idea of phylogenetic independence of sociality (Hing et al., 2018). Our study revealed a relationship between sociality and the interaction between ecological and life-history factors. This provides good evidence for a link between these correlates and sociality in this genus, which should now be tested experimentally in order to demonstrate causality. We also highlight the need for full genomic studies of *G. spilophthalmus*, *G. acicularis* and *G. ceramensis* which have caused substantial confusion in the literature at the time of writing. With continued advances in genomic sequencing we anticipate this study will encourage future research to resolve the validity of these species. Issues of species identification aside, this study complements the admirable body of research conducted on terrestrial organisms by presenting a novel perspective of ecological and life-history traits which have likely influenced the evolution of sociality. Work on terrestrial organisms has been instrumental in developing theories of social evolution. However, these terrestrially derived theories have only recently been tested against organisms displaying non-conventional life-history strategies.

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## Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jympev.2019.05.020>.

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