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The habitat preferences of *Idiosepius pygmaeus* and their use of conspecific cues

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Abstract

The two-toned pygmy squid (*Idiosepius pygmaeus*, Steenstrup, 1881) is a small, tropical cephalopod that inhabits seagrass meadows and is known to attach to blades of seagrass using a specialised adhesive organ. A global decline in seagrass habitat due to anthropogenic disturbances may threaten the species that rely on seagrass meadows for shelter, foraging and other crucial activities. It is unclear if *I. pygmaeus* can utilise alternative habitats in the absence of seagrass. Here, we test the effect of habitat type, material and composition type, and the presence of conspecifics on the settlement preferences of *I. pygmaeus*. Individuals each underwent three separate experiments: (1) testing the preference between their known habitat, *Zostera muelleri* subsp. *Capricorni* and potential substitute, *Sargassum*, (2) testing the preference to attach to a natural or artificial structure of similar shape and size, and (3) testing the preference of identical habitats, one with a conspecific adhered to and one without. We found that *I. pygmaeus* did not have a strong preference for either *Zostera* or *Sargassum*. However, a strong preference was found for attachment to the natural structure over the artificial one. There was also strong evidence for the use of conspecific cues in habitat choice, with 75% of individuals selecting the habitat that contained a conspecific. As habitat loss is the leading cause of species extinction, the knowledge of habitat preferences for *I. pygmaeus* is vital in order to assess their risk of population decline. The findings of this study suggest that *I. pygmaeus* could utilise an alternative habitat in the presence of seagrass meadow reduction, which is under threat from human activity.

KEYWORDS
behaviour, cephalopod, conspecific cues, habitat selection, macroalgae, seagrass

1 | INTRODUCTION

Habitat selection is influenced by a wide range of factors and is essential to the success and survival of a species as well as to the distribution of ecological communities. The disproportionate use of one habitat over another demonstrates a choice made by individuals based on the available conditions and resources (Mayor et al., 2009). The principle of optimal behaviour is the concept that an individual should behave in order to maximise their fitness (Pulliam, 1979). When applied to habitat selection, it assumes that an individual will select the habitat that will increase its chances of survival and reproductive success (Morris, 2003; Rosenzweig, 1981). In selecting a complex habitat, individuals often have a large amount of information to process (Meadows & Campbell, 1972) and therefore they rely heavily upon specific environmental and biological cues (Huijbers et al., 2012). In some habitats, such as seagrass meadows, there is often high structural complexity, resulting in high species richness (Stoner & Titgen, 2003). These habitats perform essential functions for marine species including provision of food, shelter from predators and performing as nursery grounds for juveniles before migrating to nearby reefs (Jackson et al., 2001; Lauria et al., 2016). In addition, seagrasses are vital to the functioning of ecosystems due to their role in carbon production and exportation, nutrient cycling and the stabilisation of sediment (Orth et al., 2006).

Within seagrass meadows, pygmy squids (*Idiosepius* spp.) have a unique association with their structural habitat. These squids readily attach to structures with an adhesive gland on their mantle (Cyran et al., 2011; Nabhitabhata, 1998; von Byern & Klepal, 2006). The genus *Idiosepius* consists of seven species and are the smallest extant cephalopods (Lu & Dunning, 1998), all of which are associated with seagrass beds (Reid & Strugnell, 2018). The two-toned pygmy squid, *Idiosepius pygmaeus* Steenstrup, 1881, is a tropical species that exhibits fast growth rates and a short lifespan (Reid & Strugnell, 2018). Males live for an average of 67 days and have an average mantle length reaching 6.5 mm at maturity, while females, on average, live for 79 days and have an average mantle length of 14.0 mm at maturity (Jackson, 1989; Reid & Strugnell, 2018). Their distribution ranges throughout the Indo-Pacific, from Northern Australia to South-East Asia (Reid & Strugnell, 2018; Rosa et al., 2019), where they inhabit seagrass meadows in shallow coastal waters (Barratt & Allcock, 2012; Moynihan, 1983). They attach to the blades of seagrass via secreting a viscous gel from an adhesive organ on the surface of their dorsal mantle (Cyran et al., 2011; Moynihan, 1983; von Byern & Klepal, 2006).

As *I. pygmaeus* inhabit inshore waters, they can be exposed to a wide range of anthropogenic disturbances (Barratt & Allcock, 2012). Their seagrass habitats are experiencing global population declines, primarily due to sediment runoff and increased nutrients, which leads to fragmentation of the seagrass meadows (Orth et al., 2006; Short et al., 2014; Short & Wyllie-Echeverria, 1996). This decline in seagrass abundance may put marine species that inhabit seagrass, including *I. pygmaeus*, at risk of population decline.

While *I. pygmaeus* is expected to use seagrass as their primary habitat, they have been observed to adhere to a variety of structures, such as prop roots, drifting leaves (Hylleberg & Nateewathana, 1991) and macroalgae (von Byern & Klepal, 2006). A common macroalgae within inshore environments is *Sargassum* spp., a brown macroalgae occurring throughout tropical and subtropical waters (Borines et al., 2013). Populations of *Sargassum* cover the benthos of shallow marine environments in the Great Barrier Reef region of Australia and provide habitats for many species (Vuki & Price, 1994). In the presence of declining seagrass, *Sargassum* may offer an alternative habitat for *I. pygmaeus*.

The shape and structure of a habitat has been found to influence habitat preference (Downes et al., 1995). *Sargassum* is similar to seagrass in shape, structure, colour and position in the water column. However, it is not clear if the composition and material of an object has an effect on attachment preference in *I. pygmaeus*. Testing the choice between a natural and artificial structure that share similarities in shape and size may demonstrate if this species has microhabitat-scale preferences.

The presence or absence of conspecifics has been suggested as a reliable cue during settlement; residents of the same species can inform settling individuals that the habitat is suitable for survival and this may reduce the costs of searching for habitat based on alternative cues (Fobert & Swearer, 2017; Stamps, 2001). In contrast, individuals may avoid sites with conspecifics due to the deleterious effects of inbreeding, density-dependent effects on growth, aggressive behaviours of residents or the increase in competition for resources (Dixson & Jones, 2018; Leis & Carson-Ewart, 2002; Rankin & Sponaugle, 2014). Due to the opposing responses to conspecifics, there are two hypotheses regarding how a species would behave when choosing a settlement site based on this cue. The 'attraction' hypothesis predicts that a settling individual would select a habitat already occupied by resident conspecifics while the 'avoidance' hypothesis predicts that conspecifics would decrease the chance of an individual settling at a site (Stamps, 1991). The behavioural response displayed by an individual towards conspecifics likely has an ecological basis that exists to enhance fitness after settlement within a chosen habitat.

The loss of habitat has been identified as the primary cause of species extinction (Venter et al., 2006; Wilcove et al., 1998) and pygmy squids could be at risk. The habitat selection and preferences of *I. pygmaeus* are not fully understood, yet by understanding this, along with knowledge of the spatial distribution of these habitats, their populations could be conserved (Lauria et al., 2016). By determining the habitat preferences of *I. pygmaeus*, the impact of seagrass loss can be better predicted. Furthermore, in understanding the role of conspecific cues in habitat settlement, development on the understanding of habitat selection in cephalopods can be made (Fletcher, 2007).

In this study, we aim to assess whether *I. pygmaeus* shows preference between their known seagrass habitat and *Sargassum* as an alternative habitat option. Furthermore, we test if the structure or material type plays a role in habitat selection by testing attachment preference between a natural wooden stick and a plastic straw of similar dimensions. Lastly, we aim to assess if *I. pygmaeus* use conspecific cues in their habitat or site attachment selection.

2 | METHODOLOGY

2.1 | Animal collection and care

Two-toned pygmy squid, *Idiosepius pygmaeus*, were collected from Cleveland Bay in Townsville, Queensland, Australia (19°15′ S, 146°49′ E) between September 18th and October 12th, 2019. Squid were captured with a triangular framed dip net, with a mesh size of 500 µm. Animals were transported to the aquarium systems at James Cook University in Townsville, Queensland. Squid were kept in rectangular tanks (39 × 29 × 29 cm) within a 10,000-L recirculating seawater system. A total of 40 squid were collected for experimental trials, with a total of 9 individuals per 25 L tank. Individuals were fed two glass shrimp (*Acetes sibogae*) per day. Glass shrimp were collected from Cleveland Bay at the same site that squid were obtained. Squid were kept in holding tanks to acclimate for 48 h before experimental trials. Acclimation times were based on previous experiments on the species showing they adjust promptly to laboratory conditions (Moltschaniwskyj et al., 2007).

2.2 | Experimental trials

The experimental tank (34 × 24 × 20 cm) had walls lined with Tuff Turf artificial grass to eliminate the possibility of squid attaching to the sides of the tank. All trials were undertaken in the same tank. The water temperature within the experimental tank was recorded before each trial using a temperature probe (Comark C26; Norfolk, UK). Temperatures during trials ranged from 26.6 to 28.0°C. A video camera (Panasonic HC-V160) was positioned directly above the tank on a tripod, recording a birds-eye-view of each trial. Three separate experiments were conducted on each individual.

2.2.1 | Experiment 1: Zostera/sargassum

We tested 40 *I. pygmaeus* individuals for preference between the seagrass, *Zostera muelleri* subsp. *Capricorni* and the macroalgae, *Sargassum* spp. Seagrass was collected from Cape Pallarenda (19°18′ S, 146°76′ E) and *Sargassum* was collected from Cleveland Bay. Portions of seagrass and *Sargassum* of similar sizes were placed at opposing ends of the tank, each covering roughly one quarter of the aquarium floor. Tanks were filled with seawater to 10 cm depth, fully submerging the habitat structures. A polyvinyl chlorine (PVC) pipe was placed upright and positioned centrally within the tank, and each squid was placed inside this pipe for a 3-min habituation period before each trial. After the habituation period, the pipe was lifted, and squid were free to move about the tank. Squid movement and behaviour was recorded for 10 min after the PVC pipe was removed.

2.2.2 | Experiment 2: Natural/artificial structures

The same individuals from experiment 1 were tested for the disproportionate use of a natural wooden stick or a plastic straw, to assess if a preference existed between different materials of similar shape and size. The same stick was used for all trials and it closely resembled the size and shape of the plastic straws (~20 cm in length and ~ 0.5 cm wide). Both a single stick and straw were placed on the surface of the water, adjacent to the length of the tank and 10 cm in from the edges. For this experiment, the depth of the water in the tank was decreased to 5 cm in order to increase the probability of the squid interacting with the materials at the surface. Again, each squid underwent 3 min of habituation within the PVC pipe prior to the commencement of the trial. Squid behaviour was filmed for 10 min after the habituation period.

2.2.3 | Experiment 3: Conspecific-occupied/unoccupied structure

Twelve *I. pygmaeus* pairs from the previous experiment were used to investigate the effect of conspecific presence on habitat choice. Here, two identical artificial plastic aquarium plants were used, each on opposite sides of the tank and comprising roughly one quarter of the area. Artificial plants were utilised in this experiment as natural habitats slightly differ in their size, shape and structural complexity, providing additional sensory cues that could influence habitat selection. The identical artificial plants control for these factors, allowing for the presence of the conspecific to be the sole cue in habitat selection. Seawater filled tanks to 10 cm depth, fully submerging the aquarium plants. To avoid mating behaviours influencing habitat choice, squid used in each trial were always of the same sex. The initial squid was placed into the PVC pipe in the centre of the tank and underwent a 3-min habituation time, after which the pipe was lifted, and the squid was able to choose a substrate to attach to. Immediately after this squid attached to either of the two habitats, a second squid was placed in the PVC pipe in the near centre of the tank, closer to the unoccupied aquarium plant, to ensure that it did not disturb the first squid. This second squid was also given a 3-min habitation time prior to the pipe being lifted. The behaviour and habitat selection of the second squid was observed and recorded during a 5-min period. Due to unequal numbers of males and females trialled per day, as well as capricious behaviours of the first squid attaching to a habitat, only 12 successful conspecific trials were completed.

2.3 | Video analyses

Videos were analysed in QuickTime Version 10.5. For trials comparing preferences between seagrass and *Sargassum*, four variables were recorded—the number of individuals attached to either *Zostera* or *Sargassum*, the time spent attached to either *Zostera* or *Sargassum*, the time spent hovering within either *Zostera* or *Sargassum* and the habitat that individuals encountered first. The time spent hovering within each habitat was defined as the squid being within the branches of the substrate. The time spent hovering was defined as the squid being a body length or more away from either habitat while swimming within the tank.

For trails comparing preferences between the natural and artificial structures, four variables were recorded—time spent attached to the stick, time spent attached to the straw, order of attachments and time spent hovering. The order of attachments involved recording which structure the squid adhered to first and continuing until their last attachment. For the conspecific trials, three variables were recorded—time taken for the first squid to attach, whether the second squid adhered to the habitat with a conspecific or whether it adhered to the empty habitat, and the time taken for the second squid to attach to this habitat. The choice of the second squid was defined as the structure that it first attached to. Data were recorded on the second squid's behaviour, including whether it interacted with both structures or the conspecific.

2.4 | Statistical analyses

Statistical analyses were performed using R statistical software and Microsoft Excel. Chi-square tests were used to assess the variation in the initial habitat choices made by *I. pygmaeus* and the probability of them remaining on their initially chosen structure or switching to the alternative structure, for both the *Zostera* and *Sargassum* trials and the stick and straw trials. A Generalised Linear Model (GLM) with a binomial distribution was used to assess if the individual's initial choice influenced whether it switched or remained on their chosen structure. Paired t-tests were used to assess the variation in time spent attached to or hovering within *Zostera* or *Sargassum* and the variation in time spent attached to the stick or straw. Chi-square tests were also used to assess the likelihood of *I. pygmaeus* settling on the habitat that is present or absent of a conspecific. A GLM with negative binomial distribution was used to determine whether the presence of a conspecific influences the time taken for an individual to attach to a chosen habitat. In all GLM's, size and sex were used as covariates.

3 | RESULTS

3.1 | Experiment 1: Zostera/Sargassum

Idiosepius pygmaeus individuals demonstrated a significant tendency to switch between habitats following their initial choice of either *Zostera* and *Sargassum*, with 29 individuals transferring between the two materials and 11 remaining at their initial habitat (Figure 1) ($x^2 = 8.1$, df = 1, $p = .004$). However, they did not show a significant preference between *Zostera* or *Sargassum* as their initial habitat choice ($x^2 = 1.6$, df = 1, $p = .2059$), with 16 individuals initially inhabiting *Zostera* and 24 selecting *Sargassum* as their first substrate. Furthermore, the tendency to switch between *Zostera* to *Sargassum* was not influenced by their initial choice of habitat ($z = -0.953$, df = 39, $p = .341$). Individuals did not significantly differ in their proportion of time attached to one habitat over the other ($t = -1.300$, df = 39, $p = .201$). However, the mean time spent both attached to and hovering within *Sargassum* was greater than that of *Zostera*, although not significantly (Figure 2). Individuals spent, on average, 287.7 (±55.9) seconds associated with *Sargassum* (153.1 ± 31.8 attached and 134.6 ± 24.1 hovering) compared with 152.9 (±58.9) seconds associated with *Zostera* (91.3 ± 27.3 attached and 61.6 ± 31.6 s hovering).

3.2 | Experiment 2: Natural/artificial structure

Of the 32 *I. pygmaeus* individuals that decided to attach to the provided structure, there was a significant preference towards the stick when first attaching to a structure, with 23 individuals selecting the stick compared with 9 that attached to the straw first (Figure 3) ($x^2 = 6.125$, df = 1, $p = .013$). From the 23 individuals that settled on the stick first, 19 of these individuals remained while four transferred to the straw. From those that attached to the straw first, seven of the nine individuals remained while two moved to the alternate habitat. The number of individuals that remained on their initial habitat, whether it be the stick or the straw, was significantly greater than those that switched structures ($x^2 = 16.000$, df = 1, $p < .001$). There was, however, no significant effect of the first choice on whether the individual decided to switch between the two materials ($z = -0.381$, df = 1, $p = .703$). There was a significant difference in the amount of time spent on each of the structures ($t = 2.168$, df = 39, $p = .036$). Individuals spent, on average more than double the amount of time attached to the stick (181.3 ± 37.6 s) compared with the straw (71.6 ± 23.3 s) per trial (Figure 4).

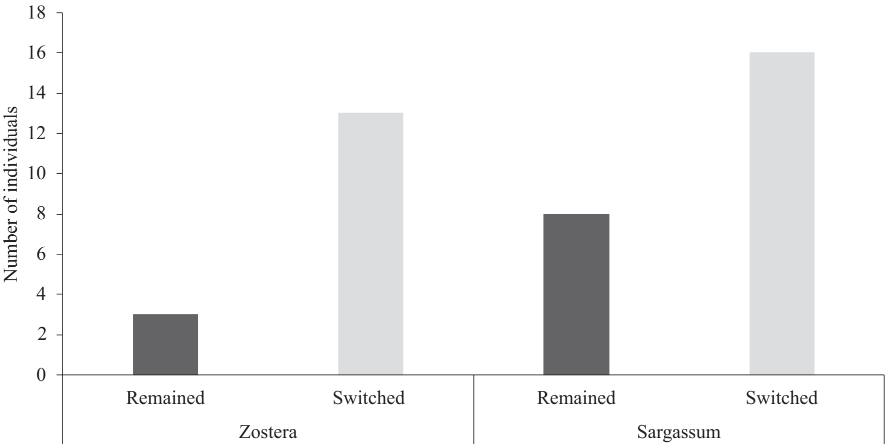

FIGURE 1 Counts of *Idiosepius pygmaeus* first inhabiting *Zostera* and remaining within this chosen habitat, inhabiting *Zostera* first and switching to *Sargassum*, inhabiting *Sargassum* first and remaining within this chosen habitat, and inhabiting *Sargassum* first and switching to *Zostera*.

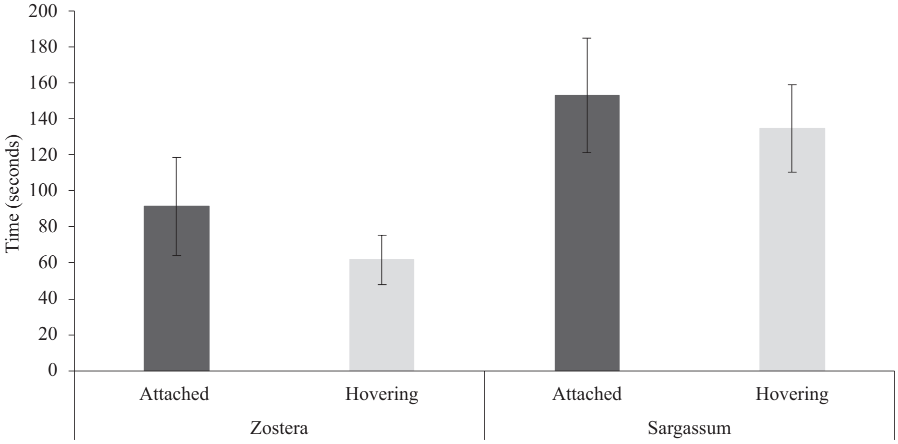

FIGURE 2 Mean time (seconds ± SE) *Idiosepius pygmaeus* spent attached to (dark grey) and hovering within (light grey) both *Zostera* and *Sargassum* habitats during experimental trials.

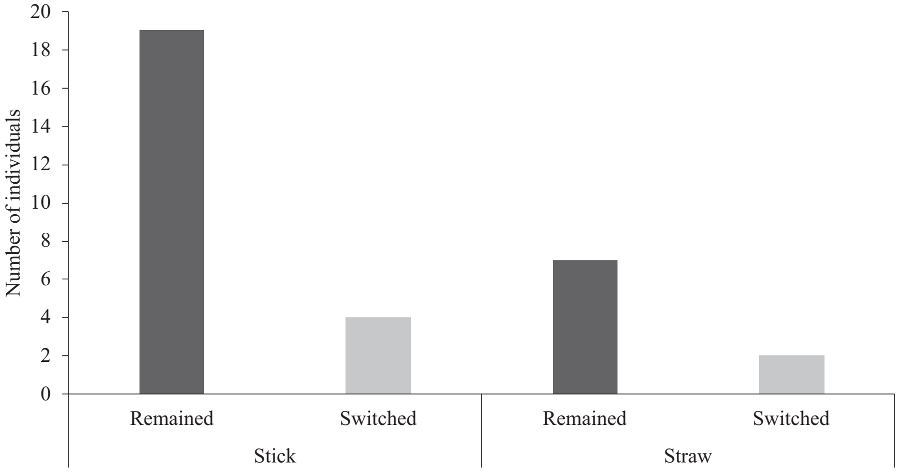

FIGURE 3 Counts of *Idiosepius pygmaeus* attaching to the stick first and remaining on this material, attaching to the stick first and switching to the straw, attaching to straw first and remaining on this material, and attaching to the straw first and switching to the stick during the experimental trial.

3.3 | Experiment 3: Conspecific-occupied/unoccupied structure

I. pygmaeus showed a significant preference for attaching to the habitat with their conspecific compared with selecting the habitat without a conspecific present (Figure 5) ($x^2 = 6.41$, df = 1, $p = .011$). From 12 trials, nine individuals selected the habitat that their conspecific was attached to, one individual selected the habitat that their conspecific was not attached to, and two did not settle on either habitat. The mean time taken by the first squid to attach to habitat was 107.2 (±43.1) s while the second squid spent an average of 64.6 (±22.0) s in the tank before settling (Figure 6). The presence of a conspecific did not significantly influence the settlement time of the second squid ($z = 1.876$, df = 18, $p = .061$); however, due to a low sample size this test had a low statistical power (power = 0.137).

4 | DISCUSSION

The two-toned pygmy squid, *Idiosepius pygmaeus*, although showing no preference between their known seagrass habitat and *Sargassum*, demonstrated a strong tendency for assessing both structures regardless of which substrate they first adhered to. In contrast, when *I. pygmaeus* was exposed to both a natural and artificial structure, individuals opted to remain on their initially chosen structure. Furthermore, *I. pygmaeus* significantly preferred the wooden stick over the plastic straw. This was demonstrated by individuals both selecting the stick initially, as well as spending significantly greater time attached to it, compared with the straw. Lastly, *I. pygmaeus* showed a strong preference for inhabiting structures that a conspecific was presently attached to, thereby supporting the use of conspecific cues and the 'attraction' hypothesis. The presence of a conspecific within a habitat resulted in a

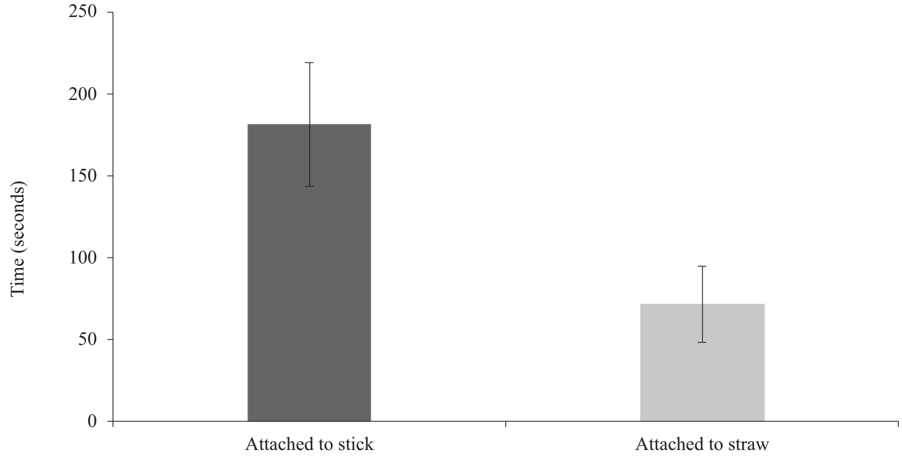

FIGURE 4 Mean time (seconds ± SE) *Idiosepius pygmaeus* spent attached to the stick (dark grey) or to the plastic straw (light grey) during experimental trials.

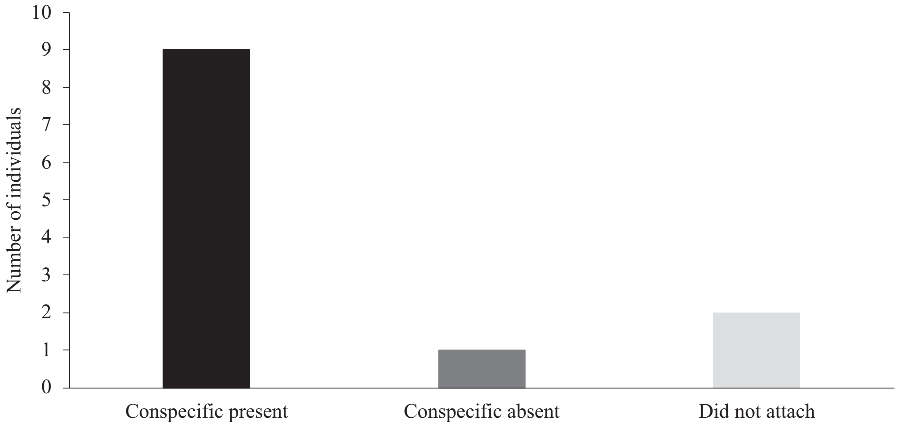

FIGURE 5 Counts of *Idiosepius pygmaeus* who settled on the habitat with a conspecific present, a conspecific absent, or did not settle on either habitat during the experimental trial.

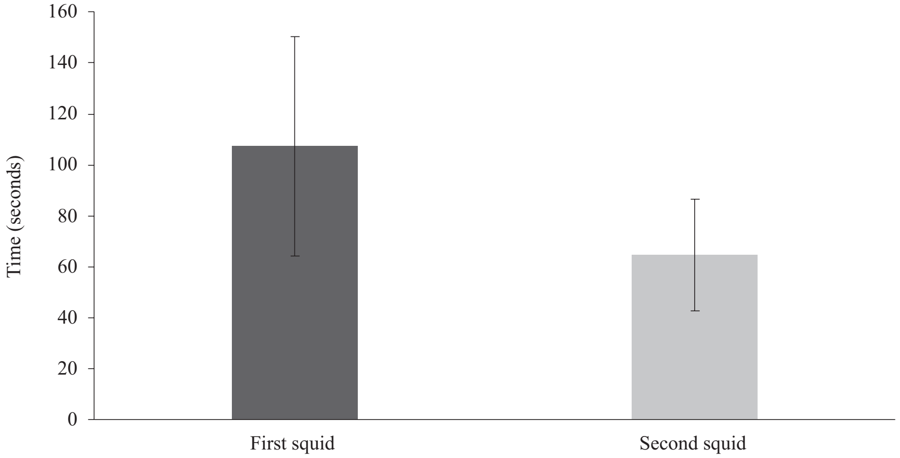

FIGURE 6 Mean time (seconds ± SE) taken by the first and second *Idiosepius pygmaeus* individual to settle on their chosen habitat during the experimental trial.

faster mean time for habitat settlement, however, this result was not statistically significant.

I. pygmaeus populations may be opportunistic in their habitat choice in response to a reduction in seagrass abundance throughout their habitat. *I. pygmaeus* occupy nearshore waters (Norman & Reid, 2000) and due to the low intensity of grazing herbivores on inshore areas along the Great Barrier Reef, the benthos is dominated by *Sargassum* (Diaz-Pulido & McCook, 2008). As seagrass meadows decline, *Sargassum* is able to immediately colonise vacant areas (den Hartog, 1997; Orth et al., 2006). *I. pygmaeus*' use of both *Zostera* and

Sargassum, with no significant preference for one over the other and a tendency to occupy both, suggests that *I. pygmaeus* could utilise *Sargassum* as an alternative habitat when facing habitat loss. *I. pygmaeus* samples in this study were collected from an area with both *Zostera* and *Sargassum* present, thus it is likely that individuals had already been exposed to both habitats. The pre-exposure to *Sargassum* in situ may have influenced the preferences of squid in their time spent attached to *Sargassum* or *Zostera*.

These results demonstrate that *Sargassum* offers a promising additional habitat for *I. pygmaeus*. However, *Sargassum*, like seagrass, is also susceptible to the destructive effects of anthropogenic activity (Noiraksar et al., 2014). If these activities are not reduced or limited, populations of *I. pygmaeus* may be affected. *Sargassum* is also strongly seasonal; it grows large canopies during the summer and reduces in size during the winter (Diaz-Pulido & McCook, 2008; Vuki & Price, 1994). Therefore, if *Sargassum* is the only available habitat for *I. pygmaeus*, their success may be affected in winter due to the reduction in available habitat. Furthermore, in response to seagrass declines, associated faunal assemblages can vary and this may have indirect impacts on populations of *I. pygmaeus* due to trophic interactions (McCloskey & Unsworth, 2015; Power, 1992).

The lack of preference between *Zostera* and *Sargassum* could be more highly influenced by their similarities in material texture rather than their similarities in structure and shape. *I. pygmaeus* showed strong variation in attachment preference between the stick and plastic straw. There was a clear preference for the wooden stick, which was the same shape and structure as the straw, but was of different material, texture and colour.

I. pygmaeus displayed a significant preference for the habitat that was already occupied by a conspecific; this finding supports the attraction hypothesis (Stamps, 1991). The structures were identical and thus one was not of higher or lower quality than the other, and all other cues used in habitat selection were homogenous. This behaviour indicates that *I. pygmaeus* receive greater benefits compared to the costs from selecting and settling onto a habitat containing an individual of the same species. The conspecific cue could aid *I. pygmaeus* in determining that the habitat is sufficient for reproduction, feeding and sheltering from predators and reduce the energetic costs of searching for another habitat (Stamps, 2001). Despite the potential costs of settlement with a conspecific, such as increased competition for resources, these are likely outweighed by the benefits of using a conspecific as a settlement cue.

Evidence for conspecific attraction has been demonstrated in a number of coral reef fish species, including damselfishes (Coppock et al., 2013, 2016; Lecchini et al., 2005; Lecchini, Planes, & Galzin, 2007; Sweatman, 1988; Wright et al., 2006), cardinalfishes (Gould et al., 2014), anemonefishes (Johnston & Dixson, 2017) and wrasses (Lecchini, Osenberg, et al., 2007, Lecchini, Planes, & Galzin, 2007). Marine invertebrates have also demonstrated conspecific attraction during settlement. In the nudibranch, *Tritonia diomedea*, a choice to travel upstream has been linked to the detection of conspecifics in that area (Wyeth & Willows, 2006) and in bobtail squid paralarvae, *Euprymna scolopes*, the presence of conspecifics was found to significantly increase the probability of settlement (Lecchini, 2011). In the selection of a habitat, various cues are used simultaneously or in an order that is dependent on the distance from the habitat (Kingsford et al., 2002). The mean time taken for the newcomer to settle between the two identical habitats was nearly 40% faster compared with that of the first squid, which did not have a conspecific present to base their selection on. While this result was slightly above the threshold of a significant result ($p = .061$), the low sample size of this test gave rise to a low statistical power, indicating the risk for a false-negative result. Therefore, it is possible that a conspecific cue does allow for a more rapid assessment of habitat quality between the two options. Additional experiments with a sufficient sample size should be conducted to confirm this. In the face of habitat loss, conspecific attraction could strengthen the ability of communities to make the shift towards a secondary habitat option.

This study demonstrates the potential for an active seagrass-associated invertebrate to utilise alternate habitat types when facing habitat decline. It also provides insight into which factors influence their habitat choice, such as material type and conspecific presence. However, it is not known if the potential alternate habitat of *Sargassum* can adequately meet the needs of *I. pygmaeus*, as the abundance of the macro-algae is seasonal and its functional uses for the species outside of shelter, such as for an egg-laying substrate, have not been demonstrated. Future studies should more thoroughly investigate if *Sargassum*, or other habitat types, are a viable alternative to their associated seagrass habitat. As habitat decline worldwide remains one of the great threats to the survival of individual species, we must determine which species are at risk and if they can demonstrate adaptive behaviours to overcome these rapid changes to their environments.

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CONFLICT OF INTEREST STATEMENT

There are no conflicts of interest held by the authors of this manuscript.

DATA AVAILABILITY STATEMENT

The authors confirm that the data presented here and that support the findings of this study are available within the article. Raw data are available on request from the corresponding author.

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