

Searching for seadragons: predicting micro-habitat use for the common (weedy) seadragon (*Phyllopteryx taeniolatus*) based on habitat and prey

Sam J. Allan¹  | Max J. O'Connell¹ | David Harasti² | O. Selma Klanten¹ | David J. Booth¹

¹Fish Ecology Lab, School of Life Sciences, University of Technology Sydney, Sydney, New South Wales, Australia

²Fisheries Research, NSW Department of Primary Industries, Port Stephens Fisheries Institute, Taylors Beach, New South Wales, Australia

Correspondence

Sam J. Allan, Fish Ecology Lab, School of Life Sciences, University of Technology Sydney, Sydney, NSW 2007, Australia.
Email: sam.allan@uts.edu.au

Abstract

Habitat associations can be critical predictors of larger-scale organism distributions and range shifts. Here the authors consider how a critical habitat, kelp (*Ecklonia radiata*) and prey (mysid crustacean swarms), can influence small- and large-scale distribution on the iconic common (weedy) seadragon (*Phyllopteryx taeniolatus*:Syn-gnathidae). *P. taeniolatus* are charismatic fish endemic to the temperate reefs of southern Australia, reported to range from Geraldton, Western Australia (28.7667°S, 114.6167°E) around southern Australia to Port Stephens, New South Wales (32.614369°S, 152.325676°E). The authors test a previously developed model of seadragon habitat preferences to predict *P. taeniolatus* occurrence within four sites from Sydney to the northern limit of their range in eastern Australia. They determined that *P. taeniolatus* associations with *Ecklonia* and mysid shrimp can be extrapolated across multiple sites to predict the occurrence of individual *P. taeniolatus* within a location/site. For instance, the authors demonstrated a significant positive relationship between the density of mysid swarms and the density of *P. taeniolatus*, evident across all sites despite large differences in the density of mysid swarms among sites. The findings are the first to model *P. taeniolatus* habitat associations across multiple sites to the northern limit of their range and have applications in protecting *P. taeniolatus* populations and how they may respond under climate change scenarios, such as poleward kelp retractions.

KEYWORDS

Ecklonia radiata, habitat associations, modelling, mysid shrimp, weedy seadragons

1 | INTRODUCTION

Predictive modelling of species distributions has long been of interest to ecologists and natural resource managers, and is a highly useful tool in ecology and conservation (Guisan & Thuiller, 2005). Species

distribution models (SDMs) have become increasingly popular in recent years to monitor the impacts of climate change (Davis *et al.*, 2021), biological invasions (Mainali *et al.*, 2015), predicting threatened species occurrence (Poulos *et al.*, 2015), and have also been used to inform IUCN Red List species assessments (Syfert

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2022 The Authors. *Journal of Fish Biology* published by John Wiley & Sons Ltd on behalf of Fisheries Society of the British Isles.

et al., 2014). SDMs are informed by modelling complex species-environment relationships (Fukuda et al., 2012). Rapid advancements in mapping the physical environment and geographical information systems (GIS) have increased the capabilities of SDMs, making it easier to obtain environmental data (Elith & Leathwick, 2009). Nonetheless, in areas where GIS data may not be readily available, or where key variables that affect a species cannot be mapped in this way (e.g., prey availability), more traditional field-based surveys and statistical methods, such as generalised linear models (GLMs), are highly useful in modelling species occurrence and habitat associations and informing other current methods such as resource selection probability functions (RSPFs) (Elith & Leathwick, 2009; Keating & Cherry, 2004; Manly et al., 2007).

Collecting environmental data and biotic interactions to use as predictor variables must be carefully selected in relation to the target species biology (Elith & Leathwick, 2009; Mainali et al., 2015), as species distributions are driven by both biotic and abiotic interactions (Davis et al., 2021). For example, potential climate refugia for the kelp, *Ecklonia radiata* (hereafter *Ecklonia*), were mapped over 10 degrees of latitude on the east coast of Australia using SDMs (Davis et al., 2021). Abiotic and biotic variables, such as sea urchin density (*Centrostephanus rodgersii*), summer bottom temperature and photosynthetically available radiation, significantly predicted *Ecklonia* cover. Another example of modelling was the application of generalised linear mixed effects modelling (GLMMs) to model the occurrence and habitat preferences of the syngnathid, *Hippocampus reidi*, across three estuaries in Brazil (Aylesworth et al., 2015), showing that seahorse occurrence was strongly linked with shallow depths, warm temperatures and increased availability of holdfast structures.

Syngnathids (seadragons, pipefish, seahorses and pipehorses) are charismatic species defined by unique morphology, low densities and small home ranges (Harasti et al., 2012; Sanchez-Camara et al., 2006; Sanchez-Camara & Booth, 2004; Vincent et al., 2011). The unique biology of syngnathids renders them particularly vulnerable to the effects of habitat loss and climate change (Vincent et al., 2011). Nonetheless, there are only few published studies modelling syngnathid habitat preferences and species occurrence (Aylesworth et al., 2015; Curtis and Vincent 2005; Harasti et al., 2014; Hernández-Urcera et al., 2021). As syngnathids have been shown to be effective flagship icons for conservation and under threat worldwide (Pollom et al., 2021; Shokri et al., 2009; Vincent et al., 2011), studies that accurately detail the distribution, occurrence and habitat associations of syngnathids are critical for effective management (Vincent et al., 2011).

The common (weedy) seadragon, *Phyllopteryx taeniolatus* (Syngnathidae) Lacepede, 1804, is a distinctive fish endemic to the Great Southern Reef (GSR) of Australia. *P. taeniolatus* are reported to range from Geraldton, Western Australia (WA), to Port Stephens, New South Wales (NSW) (Edgar, 2008). Throughout their geographical range, *P. taeniolatus* are reported to occupy different habitats such as kelps and seagrass (Kuitert, 2009; Klanten et al., 2020). Nonetheless, in Sydney, towards the northern extent of their distribution, *P. taeniolatus* are strongly associated with *Ecklonia* habitat and mysid prey (Allan et al., 2021; Sanchez-Camara et al., 2006). Mysid shrimp

(*Mysida* spp.) make up >80% of the diet of *P. taeniolatus* (Kendrick & Hyndes, 2005). It is currently unknown if changes in habitat may affect vulnerable *P. taeniolatus* populations, such as those at the northern extent of their range. Modelling has shown that under more extreme climate change scenarios, kelp declines on the east coast of Australia may be exacerbated (Castro et al., 2020; Martínez et al., 2018). Declines of other critical marine habitats have been linked to declines in abundance of other syngnathid species (Correia et al., 2015; Harasti, 2016). Extensive destruction of seagrass habitat was linked to 73% decline of *Hippocampus hippocampus* and a 94% decline of *Hippocampus guttulatus* in the Rio Formosa, Portugal (Correia et al., 2015). Furthermore, seagrass loss driven by urbanisation in Malaysia caused significant declines in *Hippocampus kuda* abundance (Vincent et al., 2011), while declines in the endangered *Hippocampus whitei* were directly linked to declines in soft coral and sponge habitat (Harasti, 2016).

Modelling habitat requirements of *P. taeniolatus* across multiple sites throughout their northern range has not been done and is essential to assist with conservation and management. To date, studies assessing habitat use of *P. taeniolatus* have only been conducted in Sydney, primarily at Kurnell, NSW (Sanchez-Camara et al., 2006; Allan et al., 2021). In the present study, the authors use GLMs to analyse how well previous knowledge (Allan et al., 2021) of *P. taeniolatus* habitat preferences, mysid density and *Ecklonia* cover can be applied to predict *P. taeniolatus* occurrence within a specific location. They compare data, including habitat composition, water depth and mysid densities, from four study sites across c. 200 km of coastline in NSW, including Broughton Island, which is the northern most recorded site for *P. taeniolatus* on the east coast of Australia, and three other sites within Sydney. They also assess the relationship of *P. taeniolatus* density and mysid shrimp density at a site and among locations. Based on previous studies (Allan et al., 2021; Sanchez-Camara et al., 2006), it was expected that mysids and *Ecklonia* cover would predict *P. taeniolatus* occurrence, and that there would be a strong positive relationship between mysid density and *P. taeniolatus* density across sites.

2 | MATERIALS AND METHODS

2.1 | Ethics statement

This project was conducted in accordance with animal ethics permit UTS ACEC ETH17-1707 and NSW DPI Permit F94/696. Any handling of animals complied with Australian animal welfare laws.

2.2 | Study sites

All observations for this study were collected using scuba, from March 2020 to September 2021, and 48 dives for a total of 36.1 h were performed across all sites, with an average dive time of 44 min (± 6.5 min). This study was conducted at four different sites from

Sydney to Port Stephens, NSW, Australia (Figure 1): Kurnell, North Bondi (NB), Cabbage Tree Bay (CTB) and Broughton Island (BI). Due to the rarity and cryptic nature of *P. taeniolatus*, study sites were selected as they had known populations of *P. taeniolatus*. Kurnell and NB are previously studied locations for *P. taeniolatus* (Sanchez-Camara *et al.*, 2005; Sanchez-Camara *et al.*, 2006; Sanchez-Camara *et al.*, 2011; Sanchez-Camara & Booth, 2004), whereas no research on *P. taeniolatus* had been undertaken at CTB and BI. CTB was selected as a site based on *P. taeniolatus* occurrence data (iNaturalist, 2021) and discussions with local divers, whereas BI was selected because there were reported sightings of *P. taeniolatus* by regional experts (Harasti *pers. comm.*). BI is located approximately 15 km to the north-east of Port Stephens, NSW, Australia, and is considered the northern limit of *P. taeniolatus* on the east coast of Australia; subsequently this is the northernmost studied population of this species. All four sites had similar benthic composition, being rocky reefs where *Ecklonia* is the dominate macroalgae, interspersed with sand flats and urchin barrens. Nonetheless, sites differed topographically. Kurnell and NB have sloping rocky reefs (depths: 3–13 m, and 5–21 m, respectively) characterised by a linear *Ecklonia*–sand interface spanning the length

of the site. In contrast, CTB and BI are more three-dimensional sand flats interspersed with rock and *Ecklonia* dominating the macrophyte community. Depth range of surveys across all sites varied: 9–13 m at Kurnell; 16–21 m at NB; 9–16 m at CTB; and 14–21 m at BI. Locations of each site were accurately determined using a diver-towed GPS (Garmin eTrex10[®]) attached to a dive flag.

2.3 | Habitat composition and environmental variables

Habitat composition at each site was determined using a point-transect method (Choat & Bellwood, 1985). Eight transects, each 50 m in length, were placed haphazardly within each site. Due to differences in the site topography across sites, methodology was adjusted accordingly to avoid resampling over the same habitat. At Kurnell and NB, both having more linear reef formations, an initial transect was placed along the kelp–sand interface (c. 12 and c. 18 m depth, respectively) with three subsequent transects placed consecutively, spanning the length of the study site. The four remaining

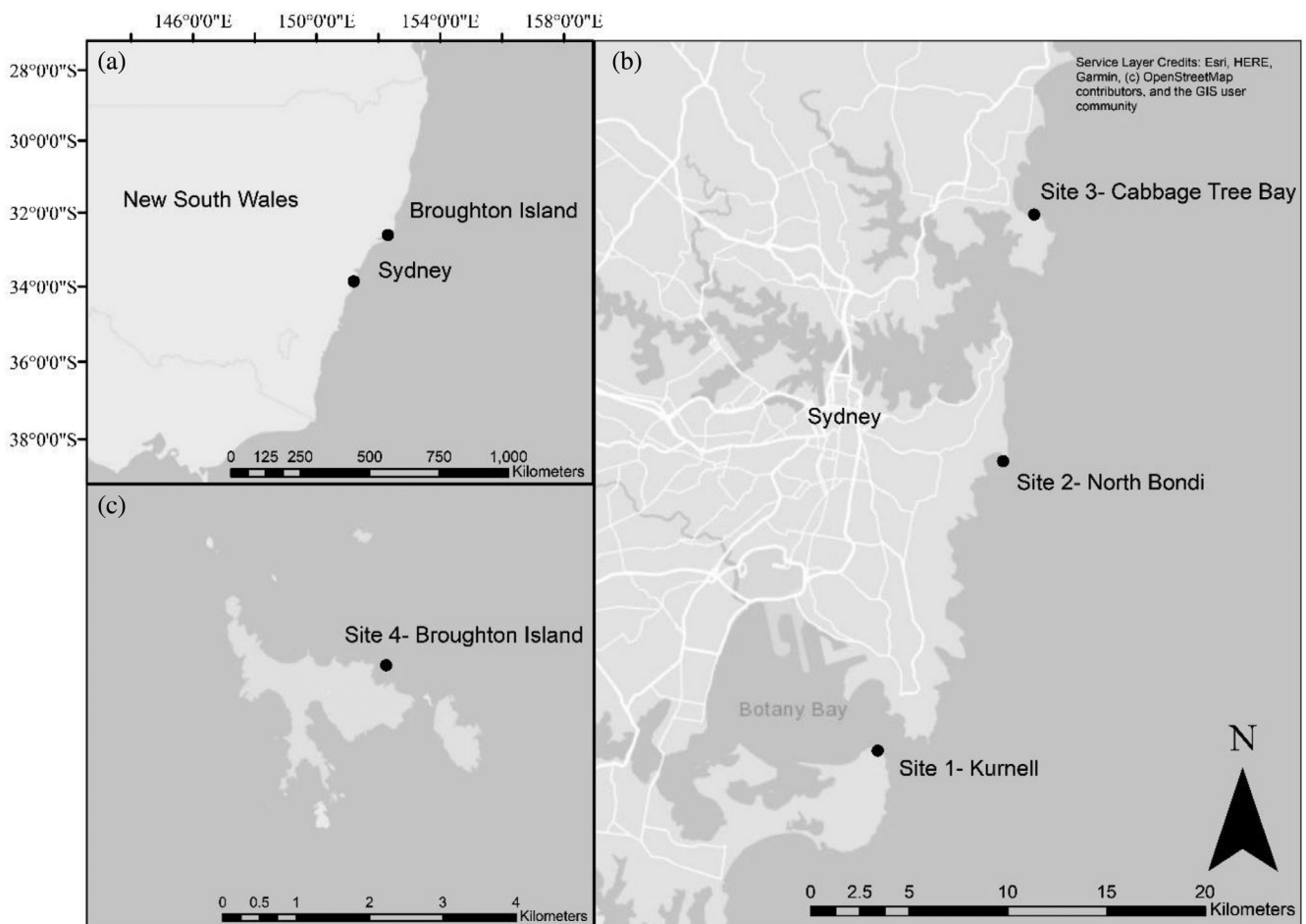


FIGURE 1 Location of *Phyllopteryx taeniolatus* survey sites from Sydney to Port Stephens, NSW, Australia. (a) Location of Broughton Island and Sydney on the east coast of Australia. (b) Location of study sites (Kurnell, North Bondi, Cabbage Tree Bay) within Sydney. (c) Location of study site on the northern side of Broughton Island

transects were placed at a parallel distance of 15 m towards the reef to ensuring all habitat was sampled. CTB and BI are more three-dimensional kelp beds, where placing four 50 m transects would run out of the survey area. Therefore, two 50 m transects were placed successively along the reef flat starting from a random point and running towards the other end of the study site, totalling eight transects. Each group of two transects was placed at a parallel distance of 15 m. Transects were filmed facing directly downwards using a GoPro 5 camera (www.gopro.com). Screenshots were taken every 1.5 m on the transect, totalling 264 images per site. Benthic percent cover was determined using Coral Point Count with Excel (CPCe) (Kohler & Gill, 2006). Benthic categories followed Allan *et al.* (2021), *i.e.*, rock, sand, sponge, *Ecklonia*, rubble, *Sargassum* spp., *Caulerpa* spp.

Additionally, depth was measured using a Suunto Zoop dive computer (www.suunto.com). If depth varied from start to endpoint of the transect, depth for that transect was recorded as an average of the two values.

2.4 | *P. taeniolatus* and mysid swarm density

Mysid shrimp swarm density and *P. taeniolatus* were determined by calculating total number of mysid swarms and *P. taeniolatus* individuals encountered along the 50 m transects (4 m wide) at each site. The total area of 8×50 m transects was 1600 m². Density estimates of *P. taeniolatus* were expressed as the number of individual seadragons per 100 m², and number of mysid swarms per 100 m². A mysid swarm was defined as a cohesive group of mysids swimming in regular spatial arrangement (Wittmann, 1977; Ohtsuka *et al.*, 1995). Several attempts were made to quantify mysid swarm size with measurements and netting techniques (Ohtsuka *et al.*, 1995). Nonetheless, due to the strong avoidance behaviours and patchy distribution of mysids (Gal *et al.*, 1999; Kaltenberg & Benoit-Bird, 2013) it was determined that this was not providing reliable and repeatable measurements for size of mysid swarms. Therefore, swarm size was not estimated, and a simple metric of swarm number/abundance was used to estimate densities.

2.5 | Predicting *P. taeniolatus* occurrence from microhabitat usage

Data on microhabitat use of *P. taeniolatus* were collected by two divers actively searching the study area at each site for *P. taeniolatus* individuals. These data were collected to test whether previous knowledge on *P. taeniolatus* microhabitat use could predict individual's occurrence within a site, across the four study sites. When each seadragon was encountered, habitat use data were collected using the methods of Allan *et al.* (2021). Five-metre-long (three-meters wide) belt transects were placed at the point of initial sighting of *P. taeniolatus* individuals and run in a haphazardly selected direction. Transects (where *P. taeniolatus* was absent) were also started haphazardly throughout the site to sample and to compare with habitat in transects with *P. taeniolatus* occurred.

Benthic cover was analysed in CPCe using the benthic categories stated above. From each 5 m transect video, three screenshots, each 5 m², were taken and analysed to determine percent cover of different benthic groups in each image, resulting in an area of 15 m² per transect. Depth and temperature were also collected at each *P. taeniolatus* sighting. Mysid swarms (defined above) were recorded as either present or absent within each transect.

2.6 | Statistical analysis

2.6.1 | Habitat composition and environmental variables

The hypothesis that habitat composition would differ across the four study sites (Kurnell, NB, CTB and BI) was tested using a one-factor permutational multivariate analysis of variance (PERMANOVA) conducted in PERMANOVA+ Version 1.0.5 within PRIMER-E 6 (Plymouth Routines in Multivariate Ecological Research; www.primers-e.com). Analysis was done on the Bray–Curtis similarity matrix with significance determined from $n = 9999$ permutations, with site analysed as a fixed factor. Depth data across all sites did not pass normality testing and therefore was analysed using a non-parametric independent samples Kruskal-Wallis test.

Additionally, habitat composition in areas where *P. taeniolatus* were present vs. absent was compared across all sites pooled and analysed with a one-factor ANOVA with a Tukey's HSD *post hoc* to discriminate variation between sites. Differences in each habitat category were then assessed among sites with ANOVA to discriminate differences in *P. taeniolatus* habitat use within each of the four study sites.

2.6.2 | *P. taeniolatus* and mysid swarm density

Mysid swarm density (number of swarms recorded on 50 m belt transect) across the four study sites was compared using a one-factor ANOVA with a Tukey's HSD *post hoc* to discriminate differences between sites. Estimates of *P. taeniolatus* density were similarly determined from the number of individuals found on each 50 m transect. The relationship of *P. taeniolatus* density and mysid availability is understudied, so this was analysed using linear regression to better understand the impact of food requirements on *P. taeniolatus* habitat selection across multiple sites. Densities were $\log_{10}(x + 1)$ transformed to ensure homoscedasticity of variance.

2.6.3 | Predicting *P. taeniolatus* occurrence from habitat preferences

GLMs were used to determine the most important variables in predicting *P. taeniolatus* occurrence within an area. A stepwise binary logistic regression model was developed in SPSS (IBM Corp 2020) to predict

P. taeniolatus presence within a site. *P. taeniolatus* presence/absence (coded 1/0) within 5 m microhabitat transects was fitted as the binary response variable. The environmental variables included in the model as predictors were based on previous results of habitat preferences of *P. taeniolatus* (Allan et al., 2021) and added to potentially increase the model's predictive value across the four study sites. Variables included in the full model were percent cover of *Ecklonia*, sand and rock, mysid presence/absence, site and depth (m) analysed as fixed effects. The stepwise procedure progressively simplified the model based on χ^2 tests. Non-significant terms were removed if they did not affect the deviance of the model (Aylesworth et al., 2015). Data from all sightings were pooled for

analysis, to increase statistical power of the study (Allan et al., 2021; Sanchez-Camara et al., 2006); nonetheless, there were too few sightings of *P. taeniolatus* to compare differences between sexes, life stages or reproductive phases.

3 | RESULTS

3.1 | Habitat composition across sites

Habitat composition did not significantly differ across sites (PERMANOVA, $F_{1,31} = 2.914$, $P > 0.05$; Figure 2). Average percent

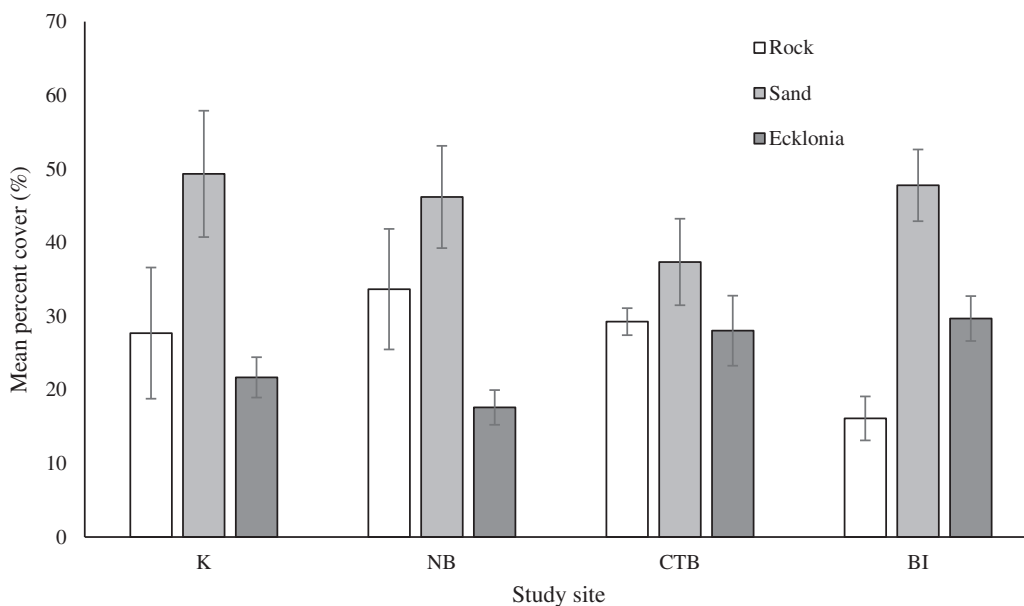


FIGURE 2 Mean (\pm S.E.) percent cover of major benthic categories, estimated from eight 50 m belt transects, at four sites from Sydney to Port Stephens, NSW, Australia (K, Kurnell; NB, North Bondi; CTB, Cabbage Tree Bay; BI, Broughton Island)

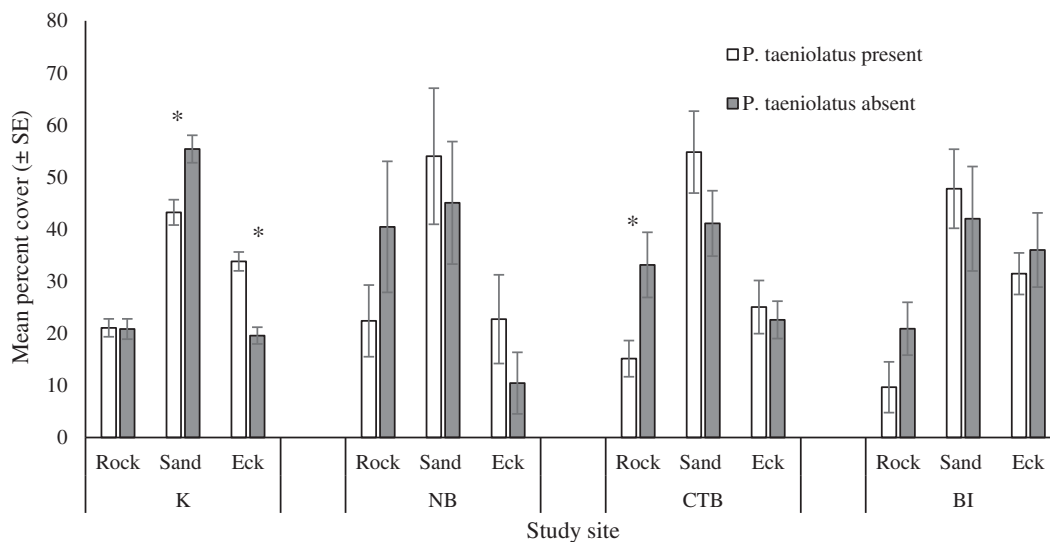


FIGURE 3 Mean percent cover of *Phyllopteryx taeniolatus* microhabitats (\pm S.E.) for the main three habitat groups (Ecklonia, sand and rock) across all study sites in NSW, Australia (K, Kurnell; NB, North Bondi; CTB, Cabbage Tree Bay; BI, Broughton Island). White bars represent mean habitat cover with *P. taeniolatus* present and grey bars where *P. taeniolatus* were absent (* indicates significant difference within sites)

cover of the main benthic categories across all sites was 27% rock, 45% sand and 24% *Ecklonia*. All habitat categories were included in the analysis, but only the dominant three habitats are represented in Figure 2. Furthermore, average depth differed across all sites (Kruskal-Wallis, $H_3 = 68.962$, $P < 0.05$). Mean depths at all sites were as follows: Kurnell, 11.2 m (± 0.3 m); NB, 18.3 m (± 0.6 m); CTB, 12.8 m (± 0.3 m); and BI, 18.6 m (± 0.3 m). Pair-wise comparisons showed depth did not differ between Kurnell and CTB ($H_3 = -6.375$, $P > 0.05$), and between NB and BI ($H_3 = 2.000$, $P > 0.05$).

Habitat composition where *P. taeniolatus* were “present” vs. “absent” differed significantly across four sites, with the former having lower rock (present = 19.51%, absent = 24.80%, $T_{204} = -2.106$, $P < 0.05$; Figure 3), and higher *Ecklonia* (present = 31.38%, absent = 20.80%, $T_{204} = 4.740$, $P < 0.05$; Figure 3). Sand did not differ significantly between areas where *P. taeniolatus* were present and absent (present = 46.37%, absent = 50.58%, $T_{204} = -1.276$, $P > 0.05$; Figure 3).

3.2 | *P. taeniolatus* vs. mysid swarm density

Pooling 50 m transects within a site (8×50 m), there were 28 mysid swarms observed at Kurnell, 9 at NB, 7 at CTB and 16 at BI, whereas the density of *P. taeniolatus* along the 50 m transects was highest at Kurnell, BI, CTB and NB, respectively. There was a significant positive

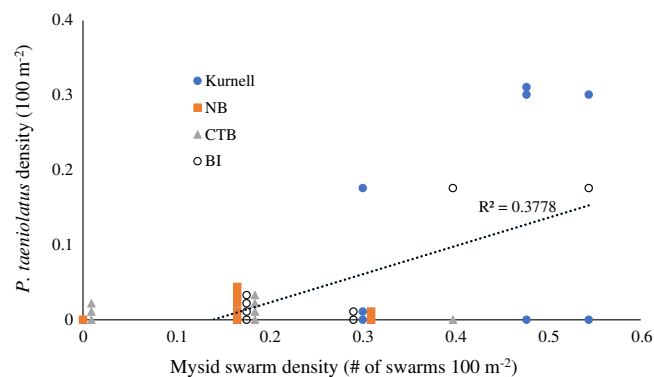


FIGURE 4 Density of *Phyllopteryx taeniolatus* individuals and mysid swarm densities along 50 m transects at four sites from Sydney to Port Stephens, NSW, Australia (K, Kurnell, blue circles; NB, North Bondi, orange squares; CTB, Cabbage Tree Bay, grey triangles; BI, Broughton Island, white circle)

TABLE 1 Final outcome of stepwise binary logistic regression model with *Phyllopteryx taeniolatus* presence/absence fitted as the response variable across four sites in NSW Australia

Effects in the model	β	Exp (β)	Exp (β) 95% C.I.	P
Mysid P/A*	1.568	4.797	2.394 – 9.613	0.0001*
<i>Ecklonia</i> % cover*	0.054	1.055	1.032 – 1.079	0.0001*
Site	0.306	1.358	0.946 – 1.951	0.10

Note: *Ecklonia* % cover, mysid P/A and site were retained in the final model as the most important effects (* indicates significance in the final model, P/A = presence/absence). Refer to Supporting Information Table for complete stepwise model. Significance indicated in bold value.

relationship between *P. taeniolatus* and mysid swarm densities across all sites ($F_{1,31} = 18.218$, $R^2 = 0.378$, $P < 0.001$; Figure 4). Furthermore, the density of mysid swarms was significantly higher at Kurnell than all other sites (Tukey's HSD *post hoc*, $P < 0.05$), whereas there was no significant difference in mysid density among the other three sites.

3.3 | Predicting *P. taeniolatus* occurrence from habitat preferences

During this study, there was a total of 114 sightings of 62 individuals of *P. taeniolatus* across all sites. GLMs determined that mysid presence/absence within a microhabitat and percent cover of *Ecklonia* were the most important variables in predicting *P. taeniolatus* presence within multiple sites (Table 1). In the exploratory stepwise analysis, the variables' sand percent cover, rock percent cover and depth were removed from the final model (Table 1). Increased percent cover of *Ecklonia* and presence of mysid shrimp both significantly increased the probability of finding an individual seadragon within a random microhabitat. Furthermore, there was no significant relationship between mysid presence and *Ecklonia* cover in the analysis ($\beta = 0.778$, $P > 0.05$). Rock was a non-significant predictor; the negative coefficient is indicative of previous findings that *P. taeniolatus* prefer areas with higher kelp and lower rock cover. Site was retained in the final model, as it did not affect the overall deviance of the model; nonetheless, it was a non-significant predictor; that is, there was no difference in habitat preferences across site. The final model predicted 71% of the variation in *P. taeniolatus* occurrence across all sites.

4 | DISCUSSION

The results show that previously developed knowledge of *P. taeniolatus* preference for *Ecklonia* habitat and mysid prey (Allan *et al.*, 2021) can be applied to predict the occurrence of *P. taeniolatus* within multiple sites over c. 200 km of coastline. Furthermore, the authors identify a significant positive relationship between the densities of mysid shrimp and *P. taeniolatus* across all study sites, despite large differences in mysid occurrence among sites.

The population of *P. taeniolatus* at Broughton Island is the reported northern limit of their range and is believed to be the most northern established population of *P. taeniolatus* on the east coast of Australia. This is the first study to assess *P. taeniolatus* at their

northern limit in NSW. As such, studying the habitat associations of range edge populations may provide critical baseline information for assessing the impacts of climate change and habitat loss on *P. taeniolatus*. The authors were expecting, given that the site is at the northern range edge, that a key predictor, such as *Ecklonia* cover or mysid density, may be low here, but not so (Davis *et al.*, 2021; Williams *et al.*, 2020). Responses of syngnathids to alterations in habitat quality and quantity, prey availability or physiological stressors may affect survival, abundance growth and reproduction of these unique fishes (Vincent *et al.*, 2011). Previously, population declines in an endangered seahorse (*H. whitei*) have been directly linked to the decline in critical habitats such as soft corals and sponges (Harasti, 2016). Therefore, the strong dependence of *P. taeniolatus* on kelp habitat and predicted shifts and declines in *Ecklonia* habitat (Castro *et al.*, 2020; Martínez *et al.*, 2018) may directly impact the persistence of *P. taeniolatus*, particularly in range edge populations. Therefore, having accurate baseline data on the range limits of *P. taeniolatus* is crucial for assessing the subsequent impacts of climate change and range shifts of associated organisms such as *Ecklonia* or mysids (Sorte *et al.*, 2010).

In this study, mean habitat composition of the three main benthic groups, sand, rock and *Ecklonia*, did not differ significantly across all sites from Sydney to Port Stephens; nonetheless, depth differed across sites. In this study, mean depth at Kurnell and CTB was shallower than that at NB and BI; nonetheless, depth was a non-significant effect in the predictive model of *P. taeniolatus* occurrence. Habitat preferences of another syngnathid, *Hippocampus reidi*, have been associated with deeper depths in the presence of increased wave action (Aylesworth *et al.*, 2015). Wave and current exposure were not included in this analysis, as this model focused on microhabitat selection, where depth and exposure were relatively uniform within a site. Nonetheless, future species distribution models for *P. taeniolatus* may benefit from including wave and current exposure of sites. As *P. taeniolatus* are poor swimmers and do not possess prehensile tails, wave and current exposure may be important factors in future models of habitat occupancy to determine new locations where *P. taeniolatus* may be present.

The distribution of *Ecklonia* extends to c. 27°S on the east coast of Australia (Wernberg *et al.*, 2019), with areas adjacent to the north of Port Stephens having comparable *Ecklonia* cover to BI (Williams *et al.*, 2020), the current range limit of *P. taeniolatus*. Therefore, it is likely that *Ecklonia* cover, while highly important for *P. taeniolatus* populations, may not be the primary limiting factor for the establishment of populations extending north from Port Stephens. Nonetheless, local declines in *Ecklonia* habitat from increased herbivory or urbanisation (Williams *et al.*, 2020) would possibly result in *P. taeniolatus* declines, as has been shown in *H. whitei* populations (Harasti, 2016). Additionally, the strong relationship between mysid density and *P. taeniolatus* density in this study was evident, despite differences between sites in mysid density. Surveying sites of similar habitat composition to those in this study, and assessing mysid availability, may provide valuable insight into mysid density being a potential limiting factor in *P. taeniolatus*

latitudinal distribution, as sites with few mysid swarms in this study had similarly lower number of *P. taeniolatus*. It is also possible that *P. taeniolatus* distribution may be limited by geographical barriers, such as large areas of sand devoid of kelp north of BI, certain species traits, as *P. taeniolatus* have low larval dispersal and exhibit high site-fidelity (Klanten *et al.*, 2020; Sanchez-Camara & Booth, 2004). There is currently no large-scale mapping of *Ecklonia* habitat within the observed depth range of *P. taeniolatus*, only mapping in smaller areas and predictive modelling (Davis *et al.*, 2021; Jordan, 2010; Williams *et al.*, 2020). Rigorous data on *Ecklonia* cover throughout the range of *P. taeniolatus* would allow for the development of more sophisticated species distribution models or habitat occupancy models.

This is the first study to model *P. taeniolatus* habitat associations towards the northern extent of their range over 200 km of coastline, and the first such study for any seadragon species. Studies monitoring habitat associations across large geographic areas are rare in syngnathids (Aylesworth *et al.*, 2015; Hernández-Urcera *et al.*, 2021), but may be extremely useful in the development of conservation and management strategies for vulnerable syngnathids or other species (Vincent *et al.*, 2011), especially given the high spatial differences in *P. taeniolatus* population genetics (Klanten *et al.*, 2020). Nonetheless, habitat mapping and more readily available environmental GIS data of *Ecklonia* habitat could lead to the development of more sophisticated SDMs detailing the range of *P. taeniolatus* throughout Australia. Given the highly charismatic nature, and fully protected status of *P. taeniolatus*, ensuring the protection of *Ecklonia* habitat and areas of high mysid density may be crucial to the persistence of seadragon populations in the future.

ACKNOWLEDGEMENTS

This research was funded in part by the Oatley Flora and Fauna Research Council. Particular thanks to Mitch Brennan and Helen Price for sustained diving support throughout the data collection phase of this research. Also, to Doug Senior and Tony Strazzari of Grey Nurse Dive Charters and the many other volunteers who assisted in collecting data for this project.

AUTHOR CONTRIBUTIONS

S.J.A. (corresponding author) contributed to conceptualisation of the study and study design, data acquisition, analysis and drafting of the original manuscript. M.J.O. contributed to data acquisition, analysis and critically revising the work. O.S.K. contributed to study design and conceptualisation, data analysis and critical review of the manuscript. D.H. contributed to data collection, analysis and interpretation, and critical revisions of the manuscript. D.J.B. contributed to conceptualising the study design and concept, data collection, analysis and interpretation and manuscript revisions.

DATA AVAILABILITY STATEMENT

The data sets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

ORCID

Sam J. Allan  <https://orcid.org/0000-0001-5326-4147>

REFERENCES

- Allan, S. J., O'Connell, M. J., Harasti, D., Klanten, O. S., & Booth, D. J. (2021). Space use by the endemic common (weedy) seadragon (*Phyllopteryx taeniolatus*): Influence of habitat and prey. *Journal of Fish Biology*, 10, 175–183.
- Aylesworth, L. A., Xavier, J. H., Oliveira, T. P. R., Tenorio, G. D., Diniz, A. F., & Rosa, I. L. (2015). Regional-scale patterns of habitat preference for the seahorse *Hippocampus reidi* in the tropical estuarine environment. *Aquatic Ecology*, 49, 499–512.
- Castro, L. C., Cetina-Heredia, P., Roughan, M., Dworjanyan, S., Thibaut, L., Chamberlain, M. A., ... Vergés, A. (2020). Combined mechanistic modelling predicts changes in species distribution and increased co-occurrence of a tropical urchin herbivore and a habitat-forming temperate kelp. *Diversity and Distributions*, 26, 1211–1226. <https://doi.org/10.1111/ddi.13073>.
- Choat, J. H., & Bellwood, D. R. (1985). Interactions amongst herbivorous fishes on a coral reef: Influence of spatial variation. *Marine Biology*, 89, 221–234.
- Correia, M., Caldwell, I. R., Koldewey, H. J., Andrade, J. P., & Palma, J. (2015). Seahorse (Hippocampinae) population fluctuations in the ria Formosa lagoon, South Portugal. *Journal of Fish Biology*, 87, 679–690.
- Curtis, J. M., & Vincent, A. C. (2005). Distribution of sympatric seahorse species along a gradient of habitat complexity in a seagrass-dominated community. *Marine Ecology Progress Series*, 291, 81–91.
- Davis, T. R., Champion, C., & Coleman, M. A. (2021). Climate refugia for kelp within an ocean warming hotspot revealed by stacked species distribution modelling. *Marine Environmental Research*, 166, 105267. <https://doi.org/10.1016/j.marenvres.2021>.
- Edgar, G. J. (2008). *Australian marine life: The plants and animals of temperate waters*. Sydney: New Holland Publishers.
- Elith, J., & Leathwick, J. R. (2009). Species distribution models: Ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, 40, 677–697.
- Fukuda, S., Mouton, A. M., & De Baets, B. (2012). Abundance versus presence/absence data for modelling fish habitat preference with a genetic Takagi–Sugeno fuzzy system. *Environmental Monitoring and Assessment*, 184, 6159–6171.
- Gal, G., Rudstam, L. G., & Greene, C. H. (1999). Acoustic characterization of *Mysis relicta*. *Limnology and Oceanography*, 44, 371–381.
- Guisan, A., & Thuiller, W. (2005). Predicting species distribution: Offering more than simple habitat models. *Ecology Letters*, 8, 993–1009.
- Harasti, D. (2016). Declining seahorse populations linked to loss of essential marine habitats. *Marine Ecology Progress Series*, 546, 173–181.
- Harasti, D., Martin-Smith, K., & Gladstone, W. (2014). Ontogenetic and sex-based differences in habitat preferences and site fidelity of White's seahorse *Hippocampus whitei*. *Journal of Fish Biology*, 85, 1413–1428. <https://doi.org/10.1111/jfb.12492>.
- Harasti, D., Martin-Smith, K., & Gladstone, W. (2012). Population dynamics and life history of a geographically restricted seahorse, *Hippocampus whitei*. *Journal of Fish Biology*, 81, 1297–1314.
- Hernández-Urcera, J., Murillo, F. J., Regueira, M., Cabanellas-Reboredo, M., & Planas, M. (2021). Preferential habitats prediction in syngnathids using species distribution models. *Marine Environmental Research*, 172, 105488.
- IBM Corp. (2020). *IBM SPSS Statistics for windows*. Armonk, NY: IBM Corp.
- iNaturalist (2021) <https://www.inaturalist.org/>
- Jordan, A., Davies, P., Ingleton, T., Foulsham, E., Nielson, J., & Prtichard, T. (2010). *Seabed habitat mapping of the continental shelf of NSW* (pp. 59–61). Sydney South: Department of Environment CCAWN.
- Kaltenberg, A. M., & Benoit-Bird, K. J. (2013). Intra-patch clustering in mysid swarms revealed through multifrequency acoustics. *ICES Journal of Marine Science*, 70, 883–891.
- Keating, K. A., & Cherry, S. (2004). Use and interpretation of logistic regression in habitat-selection studies. *The Journal of Wildlife Management*, 68, 774–789.
- Kendrick, A. J., & Hyndes, G. A. (2005). Variations in the dietary compositions of morphologically diverse syngnathid fishes. *Environmental Biology of Fishes*, 72, 415–427.
- Klanten, O. S., Gaither, M. R., Greaves, S., Mills, K., O'Keefe, K., Turnbull, J., ... Booth, D. J. (2020). Genomic and morphological evidence of distinct populations in the endemic common (weedy) seadragon *Phyllopteryx taeniolatus* (Syngnathidae) along the east coast of Australia. *PLoS One*, 15, e0243446.
- Kohler, K. E., & Gill, S. M. (2006). Coral point count with excel extensions (CPCe): A visual basic program for the determination of coral and substrate coverage using random point count methodology. *Computers geosciences*, 32, 1259–1269.
- Kuiter, R. (2009). *Seahorses and their relatives* (p. 333). Seaford, Australia: Aquatic Photographics, Kuiter R.
- Mainali, K. P., Warren, D. L., Dhileepan, K., McConnachie, A., Strathie, L., Hassan, G., ... Parmesan, C. (2015). Projecting future expansion of invasive species: Comparing and improving methodologies for species distribution modeling. *Global Change Biology*, 21, 4464–4480.
- Manly, B. F. L., McDonald, L., Thomas, D. L., McDonald, T. L., & Erickson, W. P. (2007). *Resource selection by animals: Statistical design and analysis for field studies*. Berlin: Springer Science & Business Media.
- Martínez, B., Radford, B., Thomsen, M. S., Connell, S. D., Carreño, F., Bradshaw, C. J. A., ... Wernberg, T. (2018). Distribution models predict large contractions of habitat-forming seaweeds in response to ocean warming. *Diversity and Distributions*, 24, 1350–1366.
- Ohtsuka, S., Inagaki, H., Onbe, T., Gushima, K., & Yoon, Y. (1995). Direct observations of groups of mysids in shallow coastal waters of western Japan and southern Korea. *Marine Ecology Progress Series*, 123, 33–44.
- Pollon, R. A., Ralph, G. M., Pollock, C. M., & Vincent, A. C. J. (2021). Global extinction risk for seahorses, pipefishes and their near relatives (Syngnathiformes). *Oryx*, 55, 497–506.
- Poulos, D. E., Gallen, C., Davis, T., Booth, D. J., & Harasti, D. (2015). Distribution and spatial modelling of a soft coral habitat in the Port Stephens–Great Lakes Marine Park: Implications for management. *Marine and Freshwater Research*, 67, 256–265.
- Sanchez-Camara, J., & Booth, D. J. (2004). Movement, home range and site fidelity of the weedy seadragon *Phyllopteryx taeniolatus* (Teleostei: Syngnathidae). *Environmental Biology of Fishes*, 70, 31–41.
- Sanchez-Camara, J., Booth, D. J., Murdoch, J., Watts, D., & Turon, X. (2006). Density, habitat use and behaviour of the weedy seadragon *Phyllopteryx taeniolatus* (Teleostei: Syngnathidae) around Sydney, New South Wales, Australia. *Marine and Freshwater Research*, 57, 737–745. <https://doi.org/10.1071/mf05220>.
- Sanchez-Camara, J., Martin-Smith, K., Booth, D. J., Fritschi, J., & Turon, X. (2011). Demographics and vulnerability of a unique Australian fish, the weedy seadragon *Phyllopteryx taeniolatus*. *Marine Ecology Progress Series*, 422, 253–264. <https://doi.org/10.3354/meps08920>.
- Sanchez-Camara, J., Booth, D., & Turon, X. (2005). Reproductive cycle and growth of *Phyllopteryx taeniolatus*. *Journal of Fish Biology*, 67, 133–148.
- Shokri, M. R., Gladstone, W., & Jelbart, J. (2009). The effectiveness of seahorses and pipefish (Pisces: Syngnathidae) as a flagship group to evaluate the conservation value of estuarine seagrass beds. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 19, 588–595.
- Sorte, C. J. B., Williams, S. L., & Carlton, J. T. (2010). *Marine range shifts and species introductions: Comparative spread rates and community impacts*. Hoboken: Wiley Online Library.
- Syfert, M. M., Joppa, L., Smith, M. J., Coomes, D. A., Bachman, S. P., & Brummitt, N. A. (2014). Using species distribution models to inform IUCN red list assessments. *Biological Conservation*, 177, 174–184.
- Vincent, A. C., Foster, S. J., & Koldewey, H. J. (2011). Conservation and management of seahorses and other Syngnathidae. *Journal of Fish*

- Biology*, 78, 1681–1724. <https://doi.org/10.1111/j.1095-8649.2011.03003.x>.
- Wernberg, T., Coleman, M. A., Babcock, R. C., Bell, S. Y., Bolton, J. J., Connell, S. D., ... Shears, N. T. (2019). Biology and ecology of the globally significant kelp *Ecklonia radiata*. In S. J. Hawkins, A. L. Allcock, A. E. Bates, L. B. Firth, I. P. Smith, S. E. Swearer, & P. A. Todd (Eds.), *Oceanography and Marine Biology* (pp. 265–323). Routledge: Taylor & Francis.
- Williams, J., Coleman, M. A., & Jordan, A. (2020). Depth, nutrients and urchins explain variability in *Ecklonia radiata* (laminariales) distribution and cover across ten degrees of latitude. *Aquatic Botany*, 166, 103274. <https://doi.org/10.1016/j.aquabot.2020>.
- Wittmann, K. J. (1977). *Modification of association and swarming in north Adriatic Mysidacea in relation to habitat and interacting species biology of benthic organisms* (pp. 605–612). Amsterdam: Elsevier.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Allan, S. J., O'Connell, M. J., Harasti, D., Klanten, O. S., & Booth, D. J. (2022). Searching for seadragons: predicting micro-habitat use for the common (weedy) seadragon (*Phyllopteryx taeniolatus*) based on habitat and prey. *Journal of Fish Biology*, 100(4), 935–943. <https://doi.org/10.1111/jfb.15025>