Density, habitat use and behaviour of the weedy seadragon *Phyllopteryx taeniolatus* **(Teleostei : Syngnathidae) around Sydney, New South Wales, Australia**

*Jaime Sanchez-Camara*A, *David J. Booth*B*,*E, *John Murdoch*C, *David Watts*^C *and Xavier Turon*^D

APaisajes Marinos Aquadec S.L. C/Al Salam 5, 18680 Salobreña, Granada, Spain. BDepartment of Environmental Sciences, University of Technology, Sydney, PO Box 123, Broadway, NSW 2007, Australia. CThe Sydney Aquarium, Aquarium Pier, Darling Harbour, NSW 2000, Australia. DDepartment of Animal Biology (Invertebrates), Faculty of Biology, University of Barcelona, 645 Diagonal Ave, Barcelona 08028, Spain. ECorresponding author. Email: david.booth@uts.edu.au

Abstract. The vulnerability of marine fish species, particularly those inhabiting coastal waters, is an increasingly important issue in marine conservation. Although the weedy seadragon *Phyllopteryx taeniolatus* (Lacepede, 1804), a syngnathid fish endemic to southern Australia, is legally protected in New South Wales, there are no studies on population density, habitat use and behaviour to support this protection. We investigated the abundance, sex ratios and distribution of the weedy seadragon at three sites near Sydney, Australia. The distribution, density and sex ratios of seadragons were temporally stable, suggesting no large-scale seasonal migrations. Estimated population densities varied among sites from 10 individuals per ha to 65 individuals per ha, with sex ratios close to 1 : 1. Survival rates from one encounter to the next (approximately weekly) were high, being slightly lower for males (0.985 \pm 0.006, mean \pm se) and females (0.987 \pm 0.005) compared with juveniles (1.000 \pm 0.000). All size classes and both sexes were most common near the border of kelp and sand except when exhibiting hiding behaviour, when they were more often found in kelp beds. Kelp beds were the least-used habitat when feeding. Pregnant males tended to hide more often than other groups and therefore were more frequently found in kelp and kelp patches. Seadragons tended to be solitary, although pairing and grouping behaviour was also observed. Results of the present study show that weedy seadragons are resident in the same area throughout the year and have a strong affinity with heavily weeded rock and/or sand habitat. It is therefore recommended that the current species-based protection laws be used in concert with habitat-protection zones as a necessary measure to ensure the conservation of weedy seadragon populations.

Extra keywords: common seadragon, endemic fish, grouping, habitat choice, sex ratios.

Introduction

The assessment of extinction risk to marine fishes cuts across many disciplines, including population biology, ecology and behaviour (Dulvy *et al*. 2004). Notably, species most at risk from over-fishing and habitat disturbance are those with sparse distribution, small home ranges and low fecundity (Foster and Vincent 2004), all features characteristic of syngnathids (seahorses, pipefishes, pipehorses and seadragons).

Syngnathids are a highly unusual group of fishes readily identified and positively perceived by the general public. They have the potential to act as emblematic, flagship taxa that could be used to arouse conservation concerns within the public arena. The weedy seadragon, *Phyllopteryx taeniolatus* (Lacepede), is a charismatic syngnathid that would be particularly suitable for use as an icon for conservation. Weedy seadragons are unique to southern Australian waters and the only member of the genus *Phyllopteryx* – such monotypic taxa often receive high priority in conservation policies and in evolutionary studies (Vézquez and Gittleman 1998). They are one of the largest syngnathids at up to 45 cm length (Kuiter 1993), with a distinctive shape and striking colour pattern.They are found in coastal habitats and are often observed at close quarters by recreational divers. They may also be found stranded on beaches after storms. In addition, there are long-term monitoring and educational programs based on this species (see Baker 2000; Howe 2002). The weedy seadragon is considered 'Data Deficient' on the IUCN Red List of Threatened Species (2006) and is listed as 'Lower Risk' (conservation dependent) by the Department of Environment and Heritage of Australia (Pogonoski *et al*. 2002).

Weedy seadragons are fully protected in NSW under the *Fisheries Management Act 1994* and under the Australian Commonwealth's *Environmental Protection and Biodiversity Conservation (EPBC) Act (1999)*.

Various studies of syngnathid populations exist, and although there is evidence of population declines in some species (Martin-Smith and Vincent 2005), few studies have explored the population demography of these taxa and quantified factors such as abundance, sex ratios and distribution. Even fewer have linked demography to environmental factors. For example, habitat structure may directly affect fish density by modifying the availability of shelter and food (Huston 1979; Guidetti 2000; Levi and Francour 2004). Additionally, an understanding of behaviour is becoming increasingly recognised as crucial to the success of efforts to protect populations of mobile organisms (Kramer and Chapman 1999).

Most information on distribution, density, habitat preference and behaviour of seadragons has been gathered from observations by recreational divers (Baker 2000; Howe 2002). Among other syngnathids, low population densities have been reported for seahorses, temperate pipefishes and the leafy seadragon (Foster and Vincent 2004; Curtis and Vincent 2005; Martin-Smith and Vincent 2005). Abundance data for estuarine pipefish species suggest seasonal migrations (Bayer 1980; Howard and Koehn 1985; Lazzari andAble 1990; Hiddink and Jager 2002). Sex ratio is also an important variable in a population, particularly during reproductive activity. No significant bias in the sex ratio was reported for the Australian short-headed seahorse, *Hippocampus breviceps* Peters, in Port Phillip, Victoria, Australia (Moreau and Vincent 2004) or for *Hippocampus whitei* Bleeker in a seagrass meadow in Port Jackson, New South Wales, Australia (Vincent and Sadler 1995). However, highly female-biased sex ratios were found within big-bellied seahorse, *Hippocampus abdominalis* Lesson, populations in the Derwent estuary, Tasmania (Martin-Smith and Vincent 2005). Some studies on seahorse (Bell *et al*. 2003) and pipefish species (Gronell 1984; Takahashi *et al*. 2003) reported sex ratios of 1 : 1 or skewed towards males or females depending on the area or the time of study, whereas other studies on pipefish species (e.g. Bayer 1980) reported highly female-biased sex ratios. Biased sex ratios may have implications for mate finding (Gronell 1984).

Although behavioural studies on syngnathids have primarily focussed on sexual behaviour (e.g. Berglund and Rosenqvist 1993; Masonjones and Lewis 1996; Kvarnemo *et al*. 2000), foraging behaviour has received little attention but is a key aspect of habitat use by fishes (Fulton and Bellwood 2002). Social behaviour varies among syngnathid taxa, with seahorses (see review in Foster and Vincent 2004) and pipefishes (e.g. Gronell 1984; Vincent *et al*. 1995) showing variability in degree of pairing and grouping depending on the species. Although weedy seadragons are thought to be solitary (Kuiter 2000), pairing and grouping is commonly observed. Local divers have reported groups of up to 37 individuals at or near the study sites (Howe 2002).

Dulvy *et al*. (2003) reported that 37% of all marine population extinctions (locally, regionally or globally) are caused by habitat loss. Kuiter (2001) proposed habitat degradation as the main threat to syngnathid populations because they are often found in coastal areas where anthropogenic disturbances tend to be most frequent and severe.

The most common habitat for syngnathids worldwide is seagrass (see review Foster and Vincent 2004; Moreau and Vincent 2004; Curtis and Vincent 2005). The leafy seadragon, *Phycodurus eques* Günther, was shown to prefer *Posidonia* seagrass habitat over *Amphibolis* seagrass (Connolly *et al*. 2002*a*). Edgar (2000) reports that weedy seadragons live on kelp (*Ecklonia*)-dominated reefs.

Strong site fidelity, combined with a low annual reproductive output is likely to make weedy seadragons especially vulnerable to habitat loss and limitation of food resources (Sanchez-Camara *et al*. 2005). Although a detailed description of the life history of weedy seadragons was recently provided (Forsgren and Lowe 2006), we identified a deficit of formally collated information on distribution, abundance, habitat preference and behaviour of weedy seadragons. The aim of this study was to measure abundance, sex ratios, encounter rates and survival of weedy seadragons in different locations over 1 year. We predicted that the distribution of fish would be determined by their habitat preference, which will in turn vary according to their behaviour and reproductive needs. This information was then interpreted in the light of management of this unique Australian fish.

Material and methods

Study sites

Tagging and observation took place at three sites around Sydney, NSW, Australia. At each site, we established a transect following the interface between reef and sand. These transects were parallel to the coastline, 350 m in length and were surveyed to include habitat up to 10 to 25 m from the transect line on each side (depending on the topography), yielding an estimated area covered of approximately 1 ha per transect (see Sanchez-Camara and Booth 2004; Sanchez-Camara *et al*. 2005). The length of each transect was chosen to allow a complete census during a single dive.

The two main sites, Site 1 and Site 2, were in Botany Bay National Park, near the south head of the bay (Fig. 1). Site 1 and Site 2 were adjacent, but were monitored independently because after several surveys at Site 2, none of the tagged seadragons from Site 1 were seen there. The third site was at Bondi Beach, a few kilometres north of Sites 1 and 2 (Fig. 1). Surveying of this site started later than at Sites 1 and 2 and fewer surveys were therefore accomplished. We selected these sites as being of special interest to test future human impacts. Sites 1 and 2 are in Botany Bay, where a new airport runway was recently constructed, and are adjacent to Kurnell, where construction of a water desalination plant was recently proposed. Site 3 is only a few kilometres from the Sydney central business district, an industrialised city with a population of 4 million, and is a heavily used recreational area.

Fig. 1. Study sites near Sydney, Australia.

Tagging and identification of individuals

In order to estimate density, survival rate and encounter rate, and as part of a separate study, 92 seadragons were identified at the three sites from 28 June 2001 to 4 January 2002. Seventy individuals were marked with unique VIFE (Visual Implant Fluorescent Elastomer) marks (for identification by colour and position) and 22 individuals (five of them later tagged with VIFE) were identified using natural markings and appendage patterns. The tagging was done *in situ* on SCUBA by gently restraining the animal with one hand and injecting the tagging material with the other. No signs of adverse reaction to the tagging were observed and some individuals showed feeding behaviour immediately after tagging. Identification of natural marks and appendage patterns was done by recording damaged appendages as well as the position, right or left, of the posterior tail appendages.

Sampling protocol

All observations were conducted using SCUBA from May 2001 to June 2002. A total of 128 dives were conducted over this time with a total underwater time of 290 diver hours. On each dive at the marked sites, the transect was followed from one end to the other, with divers making regular short incursions (*<*25 m) over the rocky reef and sand flats. For each seadragon found, code (if tagged), sex group (male, female, juvenile), habitat and behaviour (as specified below) were recorded on waterproof sheets.

Density and sex ratios

Seadragon density at each site was estimated using the Schnabel estimate of abundance (Schnabel 1938) for multiple censuses, as

$$
N = \Sigma (M_{\rm t} C_{\rm t}) / \Sigma (R_{\rm t})
$$

where $N =$ estimate of the total number of individuals in a population, M_t = the number of marked individuals at time *t*, C_t = total number of individuals in the sample (marked and unmarked) at time *t*, and R_t = number of marked individuals recaptured in the sample at time *t*.

The method requires the assumption that there is no mortality during the study period (see below) and therefore only data from intensive surveying periods were included in the estimates of abundance. We used censuses from 14 October 2001 to 29 December 2002 for Site 1 $(n = 22 \text{ dives}, M_1 = 36, M_{22} = 47)$ and Site 2 $(n = 13 \text{ dives}, M_1 = 28,$ $M_{13} = 36$). To estimate density at Site 3, we used data from 2 January to 5 June 2002 ($n = 9$ dives, $M_1 = 7$, $M_9 = 10$).

Sex was estimated visually *in situ*. Males have more elongated bodies and slightly thicker tails than females, which have more compressed and deeper bodies and thinner tails (see Sanchez-Camara *et al*. 2005). Juveniles were defined as those individuals first identified before 4 January 2002 whose sex could not be determined based on external morphology. These juveniles were 25–30 cm long when first seen. Young of the year that appeared at the study sites from November 2001 to June 2002 at approximately 15 cm were classified as recruits (see Sanchez-Camara *et al*. 2005). We calculated the sex ratio for each sampling occasion when more than six adults were sighted, because this is the minimum number that could result in significant departures from a 1 : 1 sex ratio. We tested these departures using Yates-corrected χ^2 tests. The numbers of males, females and juveniles (including recruits) encountered on each dive were used to represent monthly-average sightings per hour of dive. Although not an accurate estimator of total abundance (Schnabel's method was used instead), these averages proved useful to compare abundance and sex ratios at different sites throughout the year.

We used the Cormack–Jolly–Seber (CJS) model of open populations as implemented in the MARK program to ascertain survival and encounter rates (White and Burnham 1999). Data from June 2001 to June 2002 were introduced into MARK. A general model in which both survival and encounter rate were time- and group- (female, male, juvenile) dependent, was compared with less parameterised models. These reduced models included those in which either survival and encounter rates or both were constant over time and models in which either survival or encounter rate or both were independent of group. To determine the optimal model, the AIC (Akaike's Information Criterion) was used. A bootstrap goodness-of-fit test (GOF) using 100 simulations was performed for those models with more AIC weight. The over-dispersion was estimated using the variance inflation factor \hat{c} (see Cooch and White 2006).

Habitat preference and behaviour

The habitat within each transect was categorised into six types (Table 1). The behaviours of seadragons were classed as swimming, resting, hiding or feeding. For each seadragon, the number of associated conspecifics was noted. All seadragons found together or in close proximity (less than 3–4 m) were considered as a group. All data were taken by the same person (JSC) to avoid different criteria in classifying behaviour, habitat and grouping.

Numbers of sightings were arranged in contingency tables and were analysed with log-linear models (Knoke and Burke 1991) using the Loglin routine of SYSTAT 9.0 (www.systat.com/, verified September 2006) to test for differences in habitat use relative to behaviour.The same test was used to assess differences in behaviour and habitat use among pregnant males, non-pregnant males, females, juveniles and recruits. In order to test the independence of these factors, the interactions were omitted from the full models in the log-linear analyses (see Results) and expected values of sightings were generated using an iterative process. The fit of the generated tables and the observed one was then assessed by the likelihood ratio test (Sokal and Rohlf 1981). SYSTAT also calculates the significance of the contribution of particular cells to the fit of the model, by treating in a stepwise manner the cells with the largest deviate from expectation as structural zeros and refitting the model.The increase in likelihood obtained is then assessed by a likelihood ratio test. In order to detect the cells that contribute significantly to the non-independence of the data, we followed this stepwise procedure until we obtained a

non-significant increase of fit. Data from the three sites were pooled to increase the power of the analyses and to avoid empty cells in the contingency tables.

To determine whether seadragons preferentially associated with others of the same sex or the opposite sex, we compared observed and expected frequencies of each type of pair using χ^2 .

Results

Density and sex ratios

The Schnabel estimation of abundance was (mean \pm s.e.) 48.74 ± 1.56 individuals for Site 1, 64.52 ± 6.78 for Site 2 and 9.78 ± 0.27 for Site 3. Considering that the surveyed area of each site was approximately 1 ha, estimated densities were 49 seadragons ha^{-1} at Site 1, 65 seadragons ha^{-1} at Site 2 and 10 seadragons ha−¹ at Site 3.

The average number of seadragons seen per hour across months is shown in Fig. 2, including both tagged and untagged fish.The number of seadragons seen on a single dive varied, despite similar diving conditions and dive duration, from 3 to 21 seadragons at Site 1 and from 2 to 14 at Site 2. Numbers of censused seadragons were more temporally stable at Site 3, with 2 to 7 seadragons seen per dive.

The total number of seadragons seen per hour of search was 7.12 ± 0.33 (mean \pm s.e.) for Site 1, 6.64 \pm 0.42 for Site 2 and 3.85 ± 0.41 for Site 3. No seasonal trend in the abundance of seadragons was observed at any of the three sites studied (Fig. $2a-c$). There was no significant deviation from 1 : 1 sex ratios at any of the sites (Yates-corrected χ^2 < 3.84, *P* > 0.05 in all cases), and no seasonal trends in sex ratio were observed. At Site 1, there were slightly more female than male sightings (164 males, 185 females). In contrast, sightings of males (124) were higher than sightings of females (92) at Site 2 in every month (Fig. 2*b*). At Site 3, the sample size was smaller, with 22 male and 19 female sightings.

All models that included time as a factor to estimate survival and capturability fitted poorly with our data, with weight (AIC weights) of all models including time being *<*0.0001. However, at the site with the most extended sampling period and the most tagged individuals (Site 1), there was a clear influence of group type (male, female or juvenile) on both survival and probability of encounter. Therefore, model

Fig. 2. (*a*–*c*) Monthly sightings of female (white bars) male (black bars), juvenile – including recruitment – (lined bars) and uncertain (males or females) (dotted bars) weedy seadragon (mean \pm se). Number of dives indicated above each month. (*d*) Trends in seahorse sex ratio at Site 1 (black squares), Site 2 (white circles) and Site 3 (grey diamonds) for surveys with more than 6 adults sightings.

Table 2. Results of the program MARK showing (*a***) the best supported model (based on Akaike's Information Criterion (AIC)) for each site with values of fitting and over-dispersion and (***b***) survival and encounter rate for Site 1, the site with the most extended sampling period, with more sampling occasions and more tagged individuals**

$\left(a\right)$						
	Best model	AICweight	ĉ	\boldsymbol{p}	Second best model	AICweight
Site 1	O(g)p(g)	0.849	1.002	0.5	$\mathcal{O}(p(g))$	0.151
Site 2	$\mathcal{O}(p()$	0.577	1.011	0.39	$\mathcal{O}(p(g))$	0.317
Site 3	$\mathcal{O}(p())$	0.634	1.024	0.28	$\mathcal{O}(p(g))$	0.337
(b)						
		Females		Males		Juveniles
Survival rate $(Ø)$		0.9869 ± 0.0049		0.9853 ± 0.0059		1.0000 ± 0.0000
Encounter rate (p)		0.2302 ± 0.0182		0.2047 ± 0.0189		0.1068 ± 0.0147

 $\mathcal{O}(g) \times p(g)$ (\mathcal{O} = probability of surviving from encounter to the next, $p =$ probability that, if alive and in the sample, an individual will be encountered, $g = \text{group} - \text{male}$, female or juvenile) was more than five times better supported than the next supported model (Table 2*a*). We attributed this to two factors. First, the reduced (approximately one half) probability of encounter of juveniles due to their smaller size as compared with adults (females and males) (Table 2*b*) and second, the higher survival rate of juveniles over 14 cm as compared with adults (Table 2*b*). The model fitted well with the data $(P = 0.5)$, with almost no over-dispersion $(\hat{c} = 1.002)$. Although applying the same model $(\mathcal{O}(g) \times p(g))$ to Sites 2 and 3 we also obtained higher survival rate and lower probability of encounter of juveniles, the data for these sites were better explained by the reduced model $\mathcal{O}(\ell) \times p(\ell)$ as a result of the lower number of sampling occasions and juvenile encounters at these sites. Survival rates were 1.000 ± 0.000 for Site 2 and 0.9904 ± 0.0173 for Site 3. Encounter rates were 0.1216 ± 0.012 for Site 2 and 0.5155 ± 0.067 for Site 3.

Habitat preference and behaviour

Pooling data from the three sites (574 seadragon sightings in which habitat and behaviour was recorded), 78.2% were found swimming, 4.7% resting, 6.3% hiding and 10.8% feeding. The behaviour observed was habitat dependent (Fig. 3). A log-linear model of sightings according to habitat and behaviour showed that the interaction term was significant: excluding it from the model resulted in a poor fit, as indicated by the likelihood ratio (LR) χ^2 test (LR $\chi^2 = 46.97$, d.f. = 15, *P <* 0.001). Figure 3 also depicts significant departures of particular cells in the table (combinations of behaviour and habitat) from expected if there were no significant interactions. Swimming was observed over all surfaces according to the expected proportions. Resting was observed more often than expected over kelp but less often than expected over sand. Hiding was found significantly more often than expected on

Fig. 3. Frequency of observations over each defined habitat for seadragons found (*a*) swimming, (*b*) resting, (*c*) hiding and (*d*) feeding. When the deviation of particular combinations is significant (stepwise likelihood ratio test), it is indicated with a $(+)$ or $(-)$ sign, respectively, for more or less sightings than expected.

kelp and kelp patches, whereas hiding behaviour was obviously not possible over sand. It is also noticeable that feeding was observed less often than expected over kelp but more often than expected over other habitats in the absence of kelp (Fig. 3*d*).

Fig. 4. Frequency of observations of females, non-pregnant males, pregnant males, juveniles and recruits (*a*) over each defined habitat or (*b*) swimming, resting, hiding and feeding. When the deviation of particular combinations is significant (stepwise likelihood ratio test), it is indicated with a $(+)$ or $(-)$ sign, respectively, for more or less sightings than expected.

The relationship between behaviour and the sex and maturity state of the individuals (Fig. 4) was also analysed. In the log-linear analysis of the contingency table defined by these two categorical variables, when the interaction term was excluded, the difference between the observed and the fitted matrix was significant (LR χ^2 = 33.02, d.f. = 12, *P* < 0.001). Some cells of the table resulted in a significant increment of the likelihood function when removed from the analysis (i.e. when treated as structural zeros) (Fig. 4*a*). Hiding and resting behaviours were significantly more frequent than expected in pregnant males, and feeding was more common than expected in recruits.

A similar outcome of significant dependence was found when we analysed differences in habitat preference between pregnant males, males, females and juveniles (Fig. 4*b*) (LR χ^2 = 55.52, d.f. = 20, *P* < 0.001). There was a significantly higher incidence of pregnant males over kelp, kelp patches and other habitats with kelp, which is concurrent with the observation that they display hiding behaviour more often than expected and that this behaviour was more abundant over kelp and kelp patches (see above and Fig. 3*c*). Other significant patterns were the low number of non-pregnant males found over kelp and the high number of recruits over the limit between the kelp and sand.

In total, there were 729 seadragon sightings at the study sites. Fifty-nine per cent of seadragons were seen alone,

Fig. 5. (*a*) Grouping of seadragons. Total number of seadragon sightings was 729. (*b*) Pairing of seadragons. M: male, F: female, J: Juvenile. X–R: pairs including recruits. Total number of seadragon pairs sighted was 83.

23% were seen in pairs, 12% in groups of three and 6% in groups of 4 to 7 individuals (Fig. 5). All sites showed similar grouping behaviour, with single sightings being the most common occurrence. There were no significant deviations from 1 : 1 sex ratios at any of the sites (Yates-corrected χ^2 < 3.84, *P* > 0.05 in all cases) and the distribution of sexes in the pairs found was not significantly different from random pairing (χ^2 = 0.94, *P* > 0.05). Although in general there was no seasonal variation in the number of recorded pairs, groups of three or larger, at Site 2 the number of pairs peaked from October to December at 30% (18 pairs), coinciding with the peak of reproductive activity (Sanchez-Camara and Booth 2004). Of these 18 pairs, four were pregnant males together and two were post-pregnant males. These six cases were reported in December in the same area. Five pregnant males were also found together in a kelp patch in that area during December.

Discussion

The density of seadragons was stable over time at all sites. This is contrary to the seasonal migration observed for some pipefish species (e.g. Lazzari and Able 1990; Hiddink and

Jager 2002). Population densities reported in the present study for weedy seadragons are comparable with the 57 seadragons ha−¹ estimated for the leafy seadragon, *Phycodurus eques*, atWest Island, SouthAustralia (Connolly *et al*. 2002*b*). However, they are at the lower end of the range of densities reported for seahorse and pipefish species (Foster andVincent 2004; Moreau and Vincent 2004; Curtis and Vincent 2005). It should also be noted that we chose sites with relatively high densities of seadragons. The more sheltered sites with more kelp and food (mysid crustaceans were the only prey observed during the study and these were more frequently seen at Sites 1 and 2) had higher seadragon densities than Site 3, which was more exposed.

Sex ratios were slightly skewed towards males at the most sheltered and vegetated site (Site 2), probably related to breeding advantages (e.g. protection from predators, less current and turbulence for the hatchlings), although this needs further investigation. In our study populations, sex ratios were ∼1 : 1 as observed in most seahorse and some pipefish species (e.g. Vincent and Sadler 1995; Perante *et al*. 2002; Bell *et al*. 2003; Takahashi *et al*. 2003; Moreau and Vincent 2004). This, combined with low population densities and small home ranges (Sanchez-Camara and Booth 2004), could favour monogamous behaviour, which is also consistent with the low degree of sexual dimorphism in this species. However, distribution of sexes in the pairs was random and no pair bonding was observed to support this. Genetic studies of paternity etc. are needed in order to improve our knowledge of seadragon reproductive behaviour.

Habitat preference depended on the type of activity. The presence of hiding seadragons, especially pregnant males, on kelp beds is to be expected because syngnathid species have been shown to occupy habitats that best enable them to remain inconspicuous to predators (Kendrick and Hyndes 2003). Pregnant males were found hiding more often than other seadragons and this may be attributed to the need to protect the externally carried eggs from predators (Kuiter 1988). However, contrary to the spatial distribution patterns observed over seagrass beds for many syngnathids, where individuals are found within the vegetation (Diaz-Ruiz *et al*. 2000; Kendrick and Hyndes 2003), weedy seadragons concentrated near the border of the kelp and the sand. There are several reasons that could account for this habitat preference. Weedy seadragons are free-swimming and, unlike many other syngnathids, do not have prehensile tails and thus do not use anchor points to ambush prey. They are also larger and more robust than most other syngnathids and have numerous leaflike appendages, which could reduce manoeuvrability within vegetation and result in lower prey capture success than in open water. Although the efficiency of predators typically decreases in more complex habitats (Choat 1982), the effect of habitat complexity on the syngnathids' ability to capture prey is uncertain. The presence of vegetation increased the success rates of prey capture for seahorses in one study (Flynn and Ritz 1999) but had no impact in another (James and Heck 1994). Additionally, the density of mysid shrimp observed in the border areas appeared greater than in the kelp beds. We therefore suggest that the border of the kelp and the sand is the most favourable habitat for seadragons because it provides the best compromise between camouflage and access to prey.

Seadragons tended to be solitary, although pairing and grouping behaviour was common. The number of single seadragon sightings, compared with pairs, threes and larger groups, reported in this study is higher than that reported by local divers (Howe 2002). Sightings of seadragon groups of up to 37 individuals were reported at Kurnell, where most of the present study was carried out, but it should be noted that the report was based on forms sent by different divers with different criteria. These large group sizes were not observed in the present study or in later surveys at the same sites. The highest number of seadragons recorded on a single dive was 21, and these were individuals found alone or in small groups. Pair bonding occurs in at least nine different species of seahorses, whereas larger groups have been found for *H. abdominalis*, *H. breviceps* and *H. guttulatus* (Foster and Vincent 2004; Martin-Smith and Vincent 2005). In our study, sex did not seem to determine the pairs, because male–female pairings were not more common than expected compared with random pairings. In addition, there was no evidence of pair or group bonding. Only occasionally was the same pair of seadragons observed on different sampling occasions, such as a pair of recruits that were seen together three times in exactly the same area for a period of 1 week during February. Many of the pairs and groups found in certain sheltered and vegetated areas involved pregnant males. This grouping of pregnant males may increase the survival rate of the young (Pang Quong, personal communication).

In summary, the absence of seasonality in the density and sex ratios of weedy seadragons suggests that populations of weedy seadragons in New South Wales do not undergo large-scale migrations and are resident at the same heavily vegetated rocky reefs throughout the year. These areas, including their border with the sand, are the most favourable residential and breeding areas, making the risk and effort of large-scale migration unnecessary. These favourable conditions result in high survival rates of settled juveniles. Finally, seadragons appear to have some degree of social interaction. Longer-term data are necessary to accurately evaluate longevity and age-dependent survival rates. We also recommend comparison of weedy seadragon populations both close to urban or industrialised areas and those in more remote locations to evaluate human impacts on the species.

Overall, our results indicate that weedy seadragons have a strong dependence on particular habitats, which implies a high vulnerability to habitat degradation and has implications for conservation policies. It is clearly of limited

value to legally protect the weedy seadragon without an accompanying policy of habitat preservation.

Acknowledgments

We particularly thank Juan Fritschi, David van Cuylenburg, Anna Wressnig, Krystof Tichy and Ralph Alquezar for their field assistance. We also thank Keith Martin-Smith for valuable discussion. This project was funded in part by the NSW Fisheries Scientific Committee, the PADI Foundation and the Australian Geographic Society. Time spent on this article was a generosity of Paisajes Marinos Aquadec S.L. Required permits were obtained from NSW Fisheries and previous ethics approval was obtained from the University of Technology Sydney/Royal North Shore Hospital Animal Care.

References

- Baker, J. (2000). New South Wales Dragon Search Project: Preliminary Bioregional Summary of Sighting Data January 1998–June 2000, (www.dragonsearch.asn.au/database/nswnov00/nswnov00.html, verified September 2006).
- Bayer, R. D. (1980). Size, seasonality, and sex ratios of the bay pipefish (*Syngnathus leptorhynchus*) in Oregon. *Northwest Science* **54**, 161–167.
- Bell, E. M., Lockyear, J. F., McPherson, J. M., Marsden, A. D. M., and Vincent, A. C. J. (2003). First field studies of an endangered South African seahorse, *Hippocampus capensis. Environmental Biology of Fishes* **67**, 35–46. doi:10.1023/A:1024440717162
- Berglund, A., and Rosenqvist, G. (1993). Selective males and ardent females in pipefishes. *Behavioral Ecology and Sociobiology* **32**, 331–336. doi:10.1007/BF00183788
- Choat, J. H. (1982). Fish feeding and the structure of benthic communities in temperate waters. *Annual Review of Ecology and Systematics* **13**, 423–449. doi:10.1146/ANNUREV.ES.13.110182.002231
- Connolly, R. M., Melville, A. J., and Preston, K. M. (2002*a*). Patterns of movement and habitat use by leafy seadragons tracked ultrasonically. *Journal of Fish Biology* **61**, 684–695. doi:10.1111/J.1095- 8649.2002.TB00904.X
- Connolly, R. M., Melville, A. J., and Keesing, J. K. (2002*b*). Abundance, movement and individual identification of leafy seadragons, *Phycodurus eques* (Pisces: Syngnathidae). *Marine and Freshwater Research* **53**, 777–780. doi:10.1071/MF01168
- Cooch, E., and White, G. (2006). 'MARK: A Gentle Introduction.' 4th edn.Available online at: http://www.phidot.org/software/mark/docs/ book/ [accessed 30 March 2006].
- Curtis, J. M. R., and Vincent, A. C. J. (2005). Distribution of sympatric seahorse species along a gradient of habitat complexity in a seagrassdominated community. *Marine Ecology Progress Series* **291**, 81–91.
- Diaz-Ruiz, S., Aguirre-Leon, A., and Perez-Solis, O. (2000). Distribution and abundance of *Syngnathus lousianae* and *Syngnathus scovelli* (Syngnathidae) in Tamiahua Lagoon, Gulf of Mexico. *Ciencias Marinas* **26**, 125–143.
- Dulvy, N. K., Sadovy, Y., and Reynolds, J. D. (2003). Extintion vulnerability in marine populations. *Fish and Fisheries* **4**, 25–64. doi:10.1046/J.1467-2979.2003.00105.X
- Dulvy, N. K., Ellis, J. R., Goodwin, N. B., Grant, A., Reynolds, J. D., and Jennings, S. (2004). Methods of assessing extinction in marine fishes. *Fish and Fisheries* **5**, 255–276. doi:10.1111/J.1467- 2679.2004.00158.X
- Edgar, G. J. (2000). Phylum Chordata, bony fishes, family Syngnathidae. In 'Australian Marine Life. The Plants and Animals of

Temperate Waters'. pp. 424–425. (Reed New Holland Publishers: Sydney.)

- Flynn, A. J., and Ritz, D. A. (1999). Effect of the habitat complexity and predatory style on the capture success of fish feeding on aggregated prey. *Journal of the Marine Biological Association of the United Kingdom* **79**, 487–494. doi:10.1017/S0025315498000617
- Forsgren, K. L., and Lowe, C. G. (2006). The life history of weedy seadragons, *Phyllopteryx taeniolatus* (Teleostei: Syngnathidae). *Marine and Freshwater Research* **57**, 313–322. doi:10.1071/ MF05094
- Foster, S. J., and Vincent, A. C. J. (2004). Life history and ecology of seahorses: implications for conservation and management. *Journal of Fish Biology* **65**, 1–61. doi:10.1111/J.0022-1112.2004.00429.X
- Fulton, C. J., and Bellwood, D. R. (2002). Patterns of foraging in labrid fishes. *Marine Ecology Progress Series* **226**, 135–142.
- Gronell, A. M. (1984). Courtship, spawning and social organization of the pipefish,*Corythoichthys intestinalis*(Pisces: Syngnathidae) with notes on two congeneric species. *Zeitschrift fur Tierpsychologie* **65**, $1 - 24$.
- Guidetti, P. (2000). Differences among fish assemblages associated with nearshore *Posidonia oceanica* seagrass beds, rocky-algal reefs and unvegetated sand habitats in the Adriatic Sea. *Estuarine, Coastal and Shelf Science* **50**, 515–529. doi:10.1006/ECSS.1999.0584
- Hiddink, J. G., and Jager, Z. (2002). Abundance and reproduction of Nilsson's pipefish on tidal flats. *Journal of Fish Biology* **61**(Suppl. A), 125–137.
- Howard, R. K., and Koehn, J. D. (1985). Population dynamics and feeding ecology of pipefish (Syngnathidae) associated with eelgrass beds of Western Port, Victoria. *Australian Journal of Marine and Freshwater Research* **36**, 361–370. doi:10.1071/MF9850361
- Howe, E. (2002). New South Wales Dragon Search Project: Summary of Sighting Data October 2002. Report to Environment Australia by the Marine and Coastal Community Network.
- Huston, M. (1979). A general hypothesis of species diversity. *American Naturalist* **113**, 81–101. doi:10.1086/283366
- IUCN (2006). '2006 IUCN Red List of Threatened Species.' Available online at: www.iucnredlist.org [verified October 2006].
- Kendrick, A. J., and Hyndes, G. A. (2003). Patterns in the abundance and size-distribution of syngnathid fishes among habitats in a seagrass-dominated marine environment. *Estuarine, Coastal and Shelf Science* **57**, 631–640. doi:10.1016/S0272-7714(02)00402-X
- James, P. L., and Heck, K. L., Jr (1994). The effects of habitat complexity and light intensity on ambush predation within a simulated seagrass habitat. *Journal of Experimental Marine Biology and Ecology* **176**, 187–200. doi:10.1016/0022-0981(94)90184-8
- Knoke, D., and Burke, P. J. (1991). 'Log-linear Models. Quantitative Applications in the Social Sciences, No. 20.' (Sage Publishers: Newbury Park, CA.)
- Kramer, D. L., and Chapman, M. R. (1999). Implications of fish home range size and relocation for marine reserve function. *Environmental Biology of Fishes* **55**, 65–79. doi:10.1023/A:1007481206399
- Kuiter, R. H. (1988). Note sur les soins parentaux, l'eclosion et l'elevage des dragons de mer (Syngnathidae).*Revue Francaise d'Aquariologie Herpetologie* **14**(4), 113–122.
- Kuiter, R. H. (1993). 'Coastal fishes of South-Eastern Australia.' (Crawford House: Bathurst).
- Kuiter, R. H. (2000). Genus *Phyllopteryx* Swainson, 1839. In 'Seahorses, Pipefish & Their Relatives. A Comprehensive Guide to Syngnathiformes'. pp. 75–79. (TMC Publishing: Chorleywood, UK.)
- Kuiter, R. H. (2001). Revision of the Australian Seahorses of the Genus *Hippocampus* (Syngnathiformes: Syngnathidae) with Descriptions of Nine New Species. *Records of the Australian Museum* **53**, 293–340.
- Kvarnemo, C., Moore, G. I., Jones, A. G., Nelson, W. S., and Avise, J. C. (2000). Monogamous pair bonds and mate switching in the Western Australian seahorse *Hippocampus subelongatus. Journal of Evolutionary Biology* **13**, 882–888. doi:10.1046/J.1420- 9101.2000.00228.X
- Lazzari, M. A., and Able, K. W. (1990). Northern pipefish, *Syngnathus fuscus*, occurrences over the Mid-Atlantic Bight continental shelf: evidence of seasonal migration. *Environmental Biology of Fishes* **27**, 177–185. doi:10.1007/BF00001671
- Levi, F., and Francour, P. (2004). Behavioural response of *Mullus surmuletus* to habitat modification by the invasive macroalga *Caulerpa taxifolia. Journal of Fish Biology* **64**, 55–64. doi:10.1111/J.1095- 8649.2004.00280.X
- Martin-Smith, K. M., and Vincent, A. C. J. (2005). Seahorse declines in the Derwent estuary, Tasmania in the absence of fishing pressure. *Biological Conservation* **123**, 533–545. doi:10.1016/ J.BIOCON.2005.01.003
- Masonjones, H. D., and Lewis, S. M. (1996). Courtship behaviour in the dwarf seahorse, *Hippocampus zosterae. Copeia* **3**, 634–640. doi:10.2307/1447527
- Moreau, M. A., and Vincent, A. C. J. (2004). Social structure and space use in a wild population of the Australian short-headed seahorse, *Hippocampus breviceps* Peters 1869. *Marine and Freshwater Research* **55**, 231–239. doi:10.1071/MF03159
- Perante, N. C., Pajaro, M. G., Meeuwing, J. J., and Vincent, A. C. J. (2002). Biology of a seahorse species, *Hippocampus comes* in the central Philippines. *Journal of Fish Biology* **60**, 821–837. doi:10.1111/J.1095-8649.2002.TB02412.X
- Pogonoski, J. J., Pollard, D. A., and Paxton, J. R. (2002). Chapter 4. Species conservation synopses, weedy seadragon. In 'Conservation Overview andAction Plan forThreatened and PotentiallyThreatened Marine and Estuarine Fishes'. Environment Australia, Department of Environment and Heritage, Canberra, pp. 199–201.
- Sanchez-Camara, J., and 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. doi:10.1023/B:EBFI.0000022850.33643.e3
- Sanchez-Camara, J., Booth, D. J., and Turon, X. (2005). Reproductive cycle and growth of *Phyllopteryx taeniolatus. Journal of Fish Biology* **67**, 133–148. doi:10.1111/J.0022-1112.2005. 00720.X
- Schnabel, Z. E. (1938). The estimation of the total fish population of a lake. *The American Mathematical Monthly* **45**(6), 348–352. doi:10.2307/2304025
- Sokal, R. R., and Rohlf, F. J. (1981). 'Biometry: The Principles and Practice of Statistics in Biological Research.' (W. H. Freeman and Company: New York.)
- Takahashi, E., Connolly, R. M., and Lee, S. Y. (2003). Growth and reproduction of double-ended pipefish, *Syngnathoides biaculeatus*, in Moreton Bay, Queensland, Australia. *Environmental Biology of Fishes* **67**, 23–33. doi:10.1023/A:1024416031274
- Vézquez, D. P., and Gittleman, J. L. (1998). Biodiversity conservation: does phylogeny matter? *Current Biology* **8**(11), R379–R381. doi:10.1016/S0960-9822(98)70242-8
- Vincent, A. C. J., and Sadler, L. M. (1995). Faithful pair bonds in wild seahorses, *Hippocampus whitei. Animal Behaviour* **50**, 1557–1569. doi:10.1016/0003-3472(95)80011-5
- Vincent, A. C. J., Berglund, A., and Ahnesjo, I. (1995). Reproductive ecology of five pipefish species in one eelgrass meadow. *Environmental Biology of Fishes* **44**, 347–361. doi:10.1007/BF00008250
- White, G. C., and Burnham, K. P. (1999). Program MARK: survival estimation from populations of marked animals. *Bird Study* **46**(Suppl.), 120–138.

Manuscript received 5 November 2005; revised 26 June 2006; and accepted 6 September 2006.