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Species in wildlife trade: socio-economic factors influence seahorse relative abundance in Thailand

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ABSTRACT

Unsustainable wildlife trade negatively impacts wild populations of traded species. Thus to assess these population impacts and manage trade, we need to find and characterize extant populations. Seahorses are one of the most heavily traded marine animals, with almost 6 million individuals exported worldwide annually. Thailand, the top exporter, is responsible for 88% of global export volumes of dried seahorses. Here, we sought to locate seahorse hotspots in Thailand - places where seahorses are still abundant, and elucidate predictors of these hotspots. Because seahorses have economic value, we included socio-economic parameters in addition to environmental parameters. From underwater surveys, 46 seahorses from three species were spotted at 13 of 46 sites, with *Hippocampus spinosissimus* most commonly observed. The highest seahorse densities were found off Chonburi province within the Gulf of Thailand. Seahorse density and presence were not significantly associated with habitat type, while access to market was the strongest predictor. Seahorses were less abundant in areas with a seahorse market, presumably because proximate seahorse resources in these areas are attractive commodities to extract for fishers. Intense fishing activity has already greatly impacted seahorse populations in Thailand, potentially obscuring natural habitat preferences and leading to population declines. For heavily traded species whose natural populations are already impacted, human processes may have a stronger effect on species distribution than habitat type or quality. Beyond identifying and protecting suitable habitats, the preservation of seahorse populations depends on changing human behavior in interacting with seahorses and the strict enforcement of existing fishing regulations.

1. Introduction

Unsustainable wildlife trade is one of the major challenges to conserving biodiversity in Southeast Asia (Nijman, 2009). Legal wildlife trade was valued at EUR$239.5 billion globally in 2005 alone (Engler and Parry-Jones, 2007), and though official trade volumes for wildlife exports seem large, these numbers are gross underestimates of total volume due to illegal trade and under-reporting (Rosen and Smith, 2010). Wildlife trade is incredibly difficult to track and manage because it involves large transaction volumes, movements of shipments across porous international borders and complex trade routes (Nijman, 2009). Further, as populations decline due to overexploitation, animals become rare, and thus more challenging to detect and study (Gaston and Fuller, 2007, 2008).

Studies of species distribution tend to focus on habitat type and quality in order to predict occurrence and/or relative abundance (Guisan and Zimmermann, 2000; Rosa et al., 2007; Alexiades and Fisher, 2015; Hill and Diefenbach, 2014; Landi et al., 2014). This approach serves to identify and demarcate suitable or occupied habitats for future protection (Wessels, 1999; Ferrier et al., 2004; Bailey and Thompson, 2009). Increasingly however, there is a need to consider socio-economic factors to investigate species distribution, as many threatened species are imperiled by human impacts (Pimm et al., 2014), and changing environmental conditions such as habitat loss and population declines are driven largely by human behaviors (Schultz, 2011). The population status of economically valuable species in particular, is influenced by the vagaries of market supply and demand (Burton, 1999; Bulte, 2003; Clarke et al., 2007).

Seahorses (*Hippocampus* spp.) are species of conservation concern, featuring heavily in global wildlife trade both as dried (traditional medicines or curios) and live (aquaria) specimens (Vincent et al., 2011). The seahorse trade for traditional medicine is particularly significant in Southeast Asia (Choo and Liew, 2005; Giles et al., 2006; Perry et al., 2010; Vincent et al., 2011), with more than five million dried seahorses

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exported from this region annually on average (Foster et al., 2016). The main source of dried seahorses is trawl bycatch (Baum and Vincent, 2005; Giles et al., 2006; Perry et al., 2010), while live animals are specifically targeted for capture by divers (Rosa et al., 2006; Perry et al., 2010; Laksanawimol et al., 2013). As seahorses are slow-moving, and have limited home-ranges and low fecundity relative to other fish species, they are especially prone to overfishing (Foster and Vincent, 2004), thus current harvest rates may be unsustainable (Vincent et al., 2011). In addition, seahorses are particularly sensitive to habitat degradation (Duarte, 2002; Marcus et al., 2007; Harasti, 2016), further impeding population recovery.

Official trade data indicate that Thailand is the principal source of seahorses for trade, exporting an estimated 3.0–6.5 million individuals per year from 2004 to 2011 (Foster et al., 2016). Seven seahorse species are found in Thailand (Lourie et al., 2004), including the four species, *H. trimaculatus*, *H. spinosissimus*, *H. kelloggi* and *H. kuda*, that make up more than 80% of total trade (Foster et al., 2016). These four species are categorized as vulnerable on the IUCN Red List of Threatened Species (http://www.iucnredlist.org), with their global population trends all described as decreasing (Project Seahorse, 2003; Wiswedel, 2012a, 2012b; Aylesworth, 2014). However, with a dearth of information on seahorse geographic ranges, population sizes and habitat preferences, it is difficult to assess the sustainability of current rates of exploitation in Thailand, and identify the measures needed to protect existing populations.

To address these knowledge gaps, our study focused on finding and characterizing areas of high seahorse density off the coasts of Thailand, with a view of informing future efforts to assess species distribution. Based on best available knowledge, we conducted in-water surveys to identify these seahorse "hotspots" and determine the factors that best predict the locations of other hotspots. Site data included both habitat-related, or environmental, and socio-economic parameters, such as human population density, proxies for fishing pressure and market demand for seahorses. Given the fishing pressure from Thailand's extensive trawling fleet and the high export volumes of seahorses (Perry et al., 2010; Foster et al., 2016), it is likely that several seahorse populations in the country are already impacted by human activities.

2. Materials and methods

2.1. Identifying potential seahorse sites

Few data exist for seahorse sightings in Thailand. To maximize the chances of locating significant seahorse populations, we decided to focus on sites where seahorses have been previously observed, as with other studies of rare species (Blake et al., 2016; Purcell et al., 2014). Biased sampling methods such as these can provide better initial data for rare species than systematic sampling, which tends to be constricted to small areas and have very low observation frequencies (Braunisch and Suchant, 2010). Prior to fieldwork, a concerted effort was made to collate seahorse sightings in Thailand from all available sources of information including the internet, popular media, peer-reviewed and grey publications, emails, social media, and direct contact with local divers. From the first round of inquiries we generated a shortlist of potential locations along Thailand's coastal provinces where seahorses could be found.

Additionally, we conducted informal interviews to narrow down possible survey locations and ask about seahorse population trends. From 2013 to 2014, we spoke with 37 local stakeholders including marine researchers, resource managers, conservationists, fishers, boat crew and scuba divers. When applicable, we also requested examinations of dried seahorse collections to assess the species caught in the area. Questions varied by person but usually included asking about fishing grounds (seahorse distribution) and estimations of changes to seahorse populations over the last decade (population trends). Interviews were carried out in the provinces of Phuket, Phang-nga, Trang, Satun, Nakhon Si Thammarat, Surat Thani, Chumphon, Chonburi and Trat.

Due to permit restrictions, underwater surveys were only conducted outside national parks. Over two periods, September to October 2013 and April 2014 (non-rainy seasons for survey locations), a total of 46 sites was surveyed at the following locations - Ko Tao (Surat Thani), Ban Tong Tom (Chumphon), Laem Por (Surat Thani), Khanom (Nakhon Si Thammarat), Thung Walen (Chumphon), Ao Por (Phuket), Pattaya (Chonburi), Samaesan (Chonburi), Bang Saen (Chonburi) and Ko Kood (Trat) (Fig. 1, Appendix A).

2.2. Seahorse surveys

For underwater surveys, we used methodology based on random swims, which was developed for the citizen science program iSeahorse (Project Seahorse), as part of a monitoring toolkit for wild populations of seahorses (www.iseahorse.org/trends). From preliminary surveys conducted in February 2013 in Thailand and previous studies (Bell et al., 2003; Moreau and Vincent, 2004; Curtis and Vincent, 2005; Marcus et al., 2007), we determined that seahorses were rarely observed and tended to be patchily distributed. Using random belt transects, as we did in preliminary surveys, would lead to high inter-transect variance (Caldwell and Vincent, 2012; Yasue et al., 2012) and low detection rates (Aylesworth et al., unpublished results).

Surveyors searched for seahorses during random swims while scuba diving or snorkeling and estimated distance traveled using calibrated fin-kick cycles as the effort metric. When seahorses were encountered, characteristics such as sex, reproductive state, seahorse height, and holdfast type were recorded as general information. Seahorse density was recorded as number of seahorses observed per 100 m of survey distance. Juveniles were classified based on height at 50% physical maturity from Lawson et al. (2015). One to three swims were conducted at each survey site, with mean seahorse density per site calculated for >1 swim.

2.3. Site predictors - environmental variables

The following parameters were measured for each site: concentrations of nitrate, nitrite, and phosphate, pH, salinity and water temperature. At most sites ($n = 39$ of 46), 250–300 ml of seawater was collected at survey depth for analysis at Shedd Aquarium (Chicago). We were unable to test water chemistry for sites surveyed in Chonburi province ($n = 7$ of 46) in April 2014 because of logistical difficulties with storage and transport of water samples. Instead, the API 5-in-1 Aquarium Test Strips (Mars Inc., USA), Salifert Phosphate Test Kit (Holland) and a hydrometer were used to measure water chemistry (as in Miller and Botzler, 1995; Godfrey and Sanders, 2004). Water temperature was measured at all sites with the surveyor's dive computer. As seahorse predation success depends on light availability (James and Heck, 1994), horizontal visibility was estimated underwater during surveys. Other observations recorded were habitat type (silt, rubble, sand, rock, seagrass, coral, artificial; classified according to www.reefcheck.org) and number of other syngnathids (pipefishes and pipehorses) per 100 m survey distance.

2.4. Site predictors - socio-economic data

The most recent socio-economic data publicly available from online datasets were used. To our knowledge, these were the best available sources for data at the district level. Population density per km^2 for each district was obtained from a Year 2000 census report (http://web.nso.go.th/en/census/poph/popreport_e.htm) from the National Statistical Office of Thailand. Human population density in coastal areas is negatively correlated with predatory fish abundance, indicating impacts from artisanal fisheries (Stallings, 2009). As proxies for fishing pressure, we used the number of households engaged in marine fishing per district in 2004 (http://service.nso.go.th/nso/nso_center/project/search_center/province-th.htm) and the number of fishing boats registered per district in 2011 (http://www.platalay.com/boatsurvey2554/

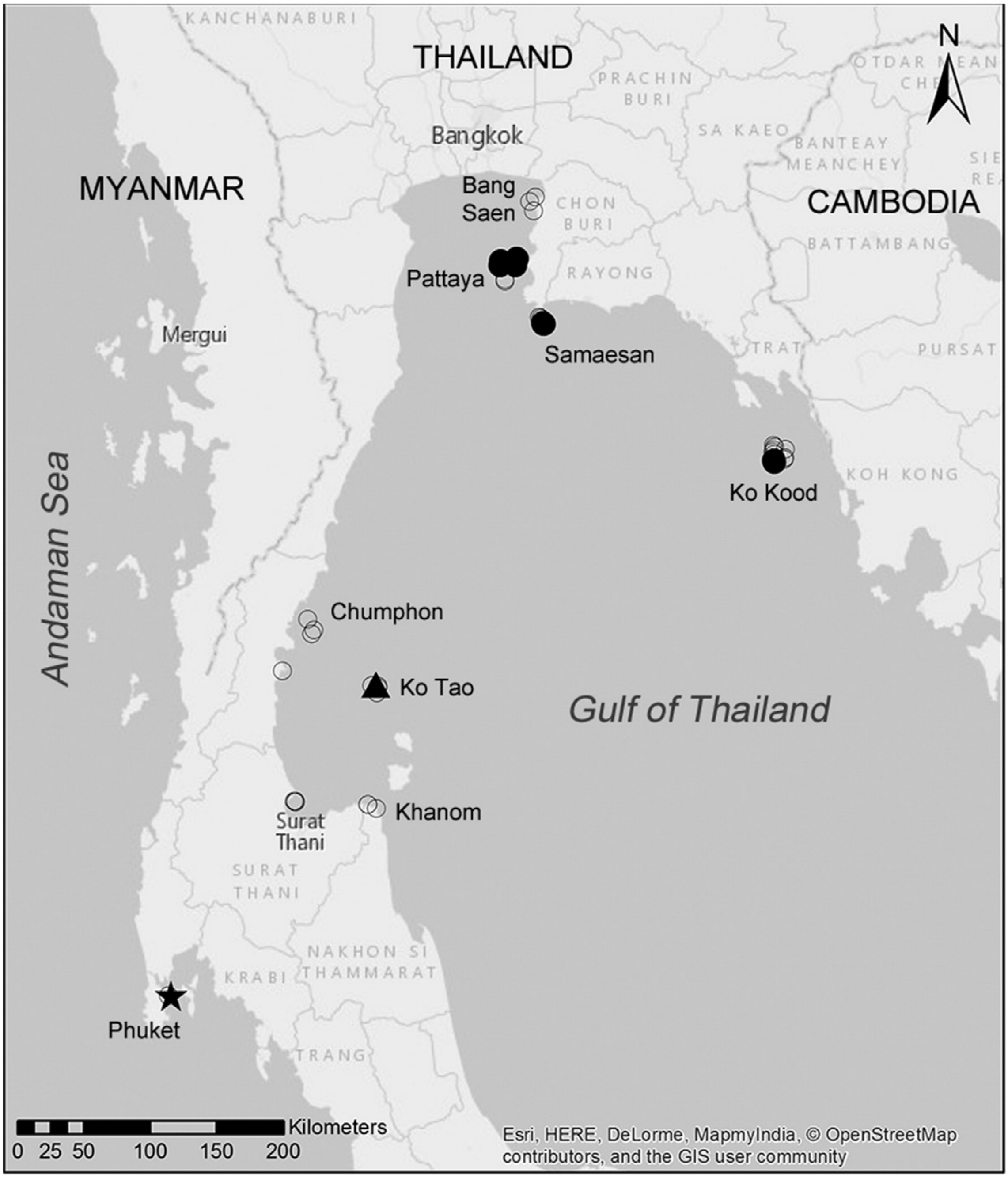

Fig. 1. Map of seahorse survey sites in Thailand. Site labels indicate: ○ - no seahorses observed, ● - *H. spinosissimus* present, ★ - *H. comes* present, ▲ - *H. kuda* present.

map.php). Access to seahorse markets within the population center closest to each survey site was scored as present or absent based on interview responses with local stakeholders such as seahorse buyers and previous research (Laksanawimol et al., 2013; Aylesworth et al., in press). The threat of overfishing and destructive fishing at each survey site was scored as low, medium or high based on extracting grid values in ArcGIS 10.2.2 from the Overfishing and Destructive Fishing layer used in the World Resources Institute's Reefs at Risk Revisited report (Burke et al., 2011).

2.5. Data analyses

To identify factors associated with seahorse occurrence and relative abundance, we ran principal coordinates and classification tree analyses using the environmental and socio-economic data for each site as input variables (Appendix B). Because seahorses have low detection rates (Issaris and Katsanevakis, 2010), they are unlikely to be spotted during surveys when numbers are low. Thus densities recorded from *in situ* surveys likely do not represent "true" population densities. Accordingly, seahorse densities per site from underwater surveys were grouped into three response categories to reflect relative abundance among sites: "Rare/Absent" for 0 seahorses/100 m, "Moderate" for ≤4 seahorses/100 m and "Abundant" for >4 seahorses/100 m (Perante et al., 2002). All multivariate analyses were carried out in R 3.3.0. A dissimilarity matrix was constructed using Gower's distance (Pavoine et al., 2009) in the package cluster (Maechler et al., 2015), followed by PCoA in the package vegan (Dixon, 2003). The significance of the principal coordinate axes in explaining proportional variance was analyzed with the broken-stick model (Peres-Neto et al., 2008). The significance of variable contribution to the ordination was tested using the envfit protocol in vegan with 999 permutations. Using seahorse abundance categories as groups, permutational multivariate analysis of variance (PERMANOVA) was then conducted with 1000 permutations to investigate among-group difference (Anderson, 2001). Additionally, the package party (Hothorn et al., 2006) was used to construct a classification tree for our data array, with “Moderate” and “Abundant” sites grouped as “Present”, as there were only three sites where seahorses were abundant. Thus seahorse “Presence” or “Rare/Absence” were used as nominal response variables. Following tree construction, we ran a Fisher's exact test with the primary factor for site classification, to test independence between sites where seahorses were present or rare/absent.

3. Results

3.1. Seahorse occurrence and relative abundance

Forty-six seahorses, 26 juveniles (all *H. spinosissimus*) and 20 adults, were found at five of the 10 survey locations- Ko Tao, Phuket, Pattaya, Samaesan and Ko Kood, and 13 of the 46 survey sites (Fig. 1). Further details by site are found in Appendix A. Three seahorse species were recorded in underwater surveys - *H. kuda*, *H. spinosissimus* and *H. comes*, the latter which is not significant in the wildlife trade but found within Southeast Asia (Lourie et al., 2004). The most common seahorse, *H. spinosissimus*, was recorded in our surveys within the Gulf of Thailand, on sand, silt, rubble and concrete artificial reef units (n = 44). *Hippocampus comes* was only found on a sponge, in sand, along the Andaman coast at Phuket (n = 1), and one individual of *H. kuda* was found over sand within the Gulf of Thailand at Ko Tao. The highest density of seahorses was found at Ko Chan, Samaesan with 10.0 seahorses/100 m surveyed, followed by Ko Lan, Pattaya with 9.1 seahorses/100 m, and Ko Pai, Pattaya with 7.3 seahorses/100 m. Individuals of *H. comes* and *H. kuda* were found at depths of 7.4–7.5 m, while the depths of *H. spinosissimus* ranged from 4.3–22.0 m (mean = 12.0 m). Seahorses were observed on a variety of holdfasts- 21 seahorses (all *H. spinosissimus*) were found on pencil sea urchins (*Prionocidaris* spp.), 13 on sponges, and the rest (n = 12) on dead coral and rubble, dead gorgonians, a twig, dead and live shells, seagrass, soft coral, a monofilament line and a nylon rope (Appendix C). Most of the juveniles (20 of 26) used pencil urchins as a holdfast; only one adult seahorse was found on an urchin. Six (all *H. spinosissimus*) of the eight adult male seahorses encountered at four sites were pregnant. Other seahorse measurements are listed in Appendix C.

Despite not encountering any in our underwater surveys, interview respondents indicated that seahorses can also be found at Ban Tong Tom (Chumphon, *H. kuda*), Laem Por (Surat Thani, *H. trimaculatus*, *H. spinosissimus* and *H. kuda*), Khanom (Nakhon Si Thammarat, species unknown), Bangsaen (Chonburi, *H. mohnikei*), and depths of 30–40 m off Pattaya (Chonburi, *H. trimaculatus*). Dried individuals of *H. trimaculatus* were observed in seahorse stockpiles at Ko Kood (Trat).

3.2. Perceptions of seahorse population trends and fisheries management

From our informal conversations with local stakeholders, most interviewees (n = 32/35) estimated that seahorse populations in their area had declined 50–90% over the past decade. Besides seahorses, there were indications that populations of other fish species have declined. In Ban Laem Prathap (Nakhon Si Thammarat), interviewees (n = 3) reported switching from fishing to agriculture and tourism, and on Ko Kood, trawl fishers (n = 2) now catch small fish for animal feed instead of fish for human consumption. Six respondents reported that trawling takes place within the 3 km trawling exclusion zone, with trawl boats coming from other provinces, and interviewees were concerned that bottom trawling would damage the shallow habitats. Trawl nets have also been found in the protected area within Mu Ko Chumphon National Park (n = 2 respondents).

3.3. Identifying predictor variables

For both PCoA and classification tree analyses, we found that habitat type did not explain seahorse presence and density at our sites. In the PCoA, the first two principal coordinate axes explained 63.9% (37.9% and 26.0% respectively) of the total variance among sites (Fig. 2), which were significant under the broken stick model. Survey sites were significantly different by seahorse abundance categories (PERMANOVA, P = 0.001). Considering the category centroids of moderate and abundant seahorse sites in the PCoA plot (Fig. 2) and variables that significantly separated sites using the envfit protocol (Table 1), moderate and abundant sites were associated with lack of access to a seahorse market, higher population density, higher phosphate levels, lower seawater temperature, fewer fishing boats, lower nitrite levels, lower salinity, and a lower threat of overfishing and destructive fishing. The relative abundance of seahorses aside, other variables that significantly separated survey sites according to envfit were the number of fishing households by district, density of other syngnathids and nitrate levels (Table 1).

The classification tree correctly classified 30 of the 46 (65.2%) survey sites (Fig. 3). Nineteen of 33 sites (57.6%) where seahorses were rare/absent and 11 of 13 sites (84.6%) where seahorses were present were classified correctly. Similar to PCoA results, the primary split was access to seahorse markets (P = 0.138), with seahorses more likely to be present where there were no markets (Fig. 3). Significantly fewer sites where seahorses were present had access to a seahorse market compared to sites where seahorses were rare or absent according to the Fisher's exact test (P = 0.019).

4. Discussion

Our study found that market access was the main predictor of seahorse abundance across our survey sites. Access to a seahorse market, an indication of demand, was a significant factor in the PCoA, and the main determining factor in the classification tree. Holding other variables constant, access to market significantly separated sites where

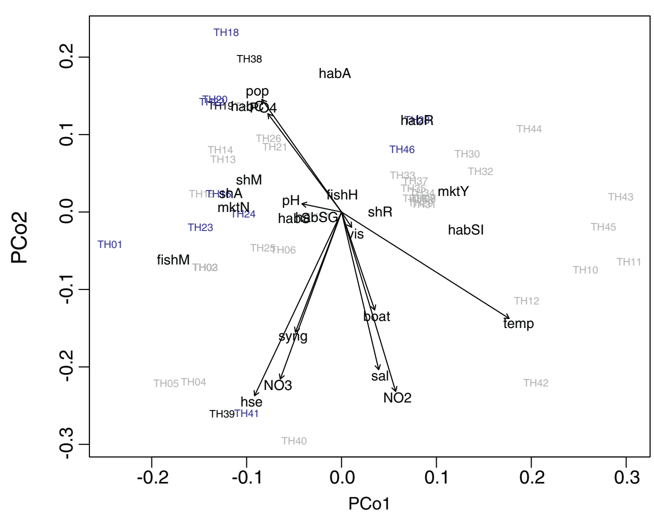

Fig. 2. Plot of principal coordinates analysis of survey sites overlaid by factors used in the ordination. Sites where seahorses are rare or absent are labeled light grey, sites with moderate seahorse density are labeled grey and sites with high seahorse density are labeled black. Continuous variables are represented by arrows, boat = number of fishing boats in the district, hse = number of fishing households in the district, syng = density of other syngnathids, vis = visibility, temp = water temperature, pH = water pH, NO2 = nitrite concentration, NO3 = nitrate concentration, PO4 = phosphate concentration, sal = *in situ* salinity, pop = population density in the district. Categorical variables have the following attributes: sh = relative abundance of seahorses (A: abundant, M: moderate, R: rare/absent), mkt = access to seahorse market (Y: yes, N: no), fish = threat of overfishing and destructive fishing (M: moderate, H: high), hab = habitat type (SI: silt, R: rubble, S: sand, RC: rock, SG: seagrass, C: coral, A: artificial).

Table 1
Association of continuous and categorical variables with the PCoA ordination of the survey sites using the envfit function in vegan. Significant variables are marked with *. P-values are based on 999 permutations. Thirteen observations were deleted due to missing values.

Continuous variables				
Variable	Dim1	Dim2	R^2	P-value
No. of fishing boats per district*	0.27	−0.96	0.19	0.045
No. of fishing households per district*	−0.36	−0.93	0.71	0.001
Density of other syngnathids*	−0.30	−0.95	0.29	0.004
Visibility	0.47	−0.88	0.01	0.913
Temperature*	0.79	−0.61	0.02	0.001
pH	−0.97	0.25	0.02	0.742
Nitrite concentration*	0.24	−0.97	0.63	0.001
Nitrate concentration*	−0.29	−0.96	0.56	0.001
Phosphate concentration*	−0.52	0.85	0.24	0.019
Salinity*	0.19	−0.98	0.47	0.001
Population density per district*	−0.50	0.87	0.31	0.003
Categorical variables			Goodness-of-fit test	
Seahorse relative abundance- abundant*	−0.12	0.02	0.17	0.023
Moderate	−0.10	0.04		
Rare/absent	0.04	0.00		
Habitat- artificial	−0.01	0.18	0.27	0.052
Coral	−0.10	0.14		
Rubble	0.08	0.12		
Sand	−0.05	−0.01		
Seagrass	−0.03	−0.01		
Silt	0.13	−0.02		
Threat of overfishing and destructive fishing - high*	0.00	0.02	0.10	0.027
Moderate	−0.18	−0.06		
Access to market - no*	−0.11	0.01	0.42	0.001
Yes	0.12	0.03		

seahorses were present and rare or absent. Supporting the trend with market access, seahorse relative abundance was also correlated with other fisheries-related factors- fewer fishing boats per district and lower estimated threat of overfishing and destructive fishing. Our results support studies identifying the targeting of species for commercial purposes as key drivers in reducing wildlife population abundance (Walsh et al., 2003; Brashares et al., 2004) and the impacts of market demand on fisheries stock size structure (Reddy et al., 2013). Similarly,

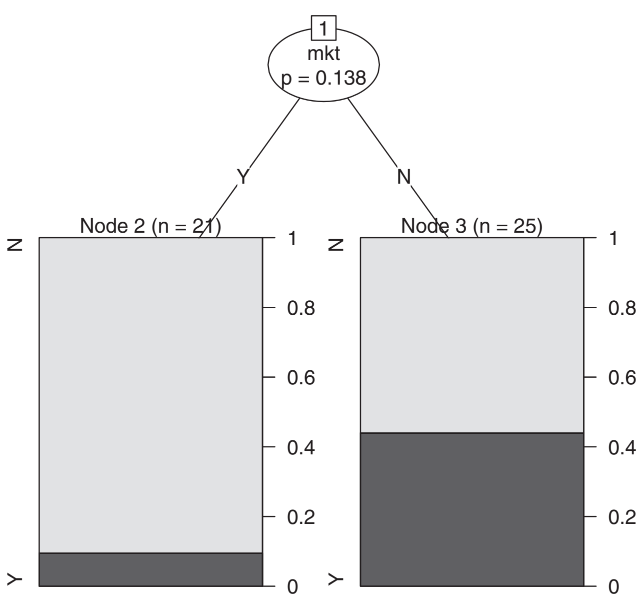

Fig. 3. Classification tree of sites where seahorses are present (Y) or rare/absent (N). Access to market was the main splitting factor. Seahorses tended to be rare/absent (Node 2) if there was access to a market near the site (Y).

Rosa et al. (2007) found that in Brazil, seahorse densities were lower in areas where seahorses were traded. The implication is that wild populations of seahorses in Thailand have been greatly impacted by increased market demand and access, leading to high levels of exploitation through targeted and non-targeted fishing (Perry et al., 2010; Laksanawimol et al., 2013). Even in 1998 and 1999, fishers and traders in Thailand reported declines in seahorse populations or catch (Perry et al., 2010). More than 10 years later, our interview respondents corroborated a similar trend of decline of at least 50% over the past decade, although these remain unverified estimates.

Seahorses inhabit a broad geographic range of shallow coastal areas, exhibiting generalist habitat preferences as a genus (Lourie et al., 2004; Teske et al., 2007). This generalist trait is supported by our finding that variability in seahorse relative abundance among survey sites were not significantly correlated with habitat type. Additionally, contrary to their reputation elsewhere as indicators of environmental quality (Shokri et al., 2009), seahorse relative abundance in our surveys did not correspond with low nutrient concentrations but was positively correlated with higher phosphate levels. Similarly, seahorses elsewhere have been shown to live in waters considered to be heavily polluted with trace metals, organic waste and hydrocarbons (Gristina et al., 2015). As in aquarium-based studies of tropical seahorses (Lin et al., 2006; Sheng et al., 2006), seahorses in our study preferred cooler seawater temperatures, though the overall temperature range was small (28–32 °C). Lower seawater salinities were also preferred, which is probably an artifact of most of the seahorses we surveyed being found at shallow, nearshore sites. We note that any underlying habitat preferences could be obscured by fishing impacts, as human influence can decouple biophysical relationships in marine environments (Williams et al., 2015). We also acknowledge that our seahorse sample size was low, as seahorses were rare and cryptic in the field. Because of their crypsis and low detection rates, we targeted areas with the highest probabilities of spotting seahorses. Compared to a random site-selection design, this may not have yielded the most robust statistical analysis, but did contribute valuable understanding of where seahorses live in order to inform conservation measures that protect these threatened species.

From surveys and interviews, seahorses can be found along the entire extent of the coastline surveyed in Thailand, including three of the four species common in trade. Both *H. spinosissimus* and *H. trimaculatus* were previously thought to inhabit depths of at least 10–15 m (Lourie et al., 1999; Choo and Liew, 2003), but their depth ranges may need to be updated. Although *H. trimaculatus* was only observed from trawl landings from depths of 25–40 m, this species has been reported from shallower depths in Thailand (L. Aylesworth, pers. obs., C. Scott, pers. comm.), Malaysia (Lim et al., 2011), Cambodia and Vietnam (T. Loh, pers. obs.), and India (Murugan et al., 2008). We also observed 16 individuals of *H. spinosissimus* at < 10 m depth at five survey sites (Appendix C). From fisher interviews, other seahorse habitats are found farther offshore at trawling grounds, which could be important areas for *H. trimaculatus*. Because surveys were conducted using SCUBA or by snorkeling, observations in this study were restricted to depths < 30 m, while deeper habitats may be more important for *H. trimaculatus.* Only one individual each of *H. comes* and *H. kuda* was found along the Andaman coast and the Gulf of Thailand respectively, but it is likely that both species inhabit both coasts of Thailand (Panithanarak et al., 2010; Lim et al., 2011).

Seahorse holdfast type is often recorded to identify important microhabitats or associated species, with the availability of specific holdfasts used to predict seahorse presence (Perante et al., 2002; Dias and Rosa, 2003; Curtis and Vincent, 2005). In our study, pencil sea urchins were most commonly employed as holdfasts, especially for *H. spinosissimus* at all five sites off Pattaya, Chonburi where seahorses were found. However, this pattern is unlikely to indicate a specific preference for pencil urchins, given the variety of substrates used as holdfasts, from biotic to man-made structures. As with habitat, the seahorses in our study exhibit generalist tendencies for holdfast types. The association between seahorses and pencil urchins is more likely opportunistic, with pencil urchins offering suitable substrate and a predator refuge in sandy habitats with low topographical complexity, particularly for juvenile seahorses.

The highest densities of seahorses were found off Chonburi province within the Gulf of Thailand, but these sites do not necessarily indicate the most optimal habitat for seahorses in Thailand. For example, seahorse populations monitored in Italy persisted not because of habitat quality, but because of a lack of fishing pressure, as the presence of mussel farms prevented trawlers from deploying fishing gear in seahorse habitats (Gristina et al., 2015). Pattaya is situated in the Banglamung district, which has the highest population density in our survey, probably contributing to the correlation between seahorse relative abundance and population in the ordination. The seahorses in Chonburi province likely comprise remnant populations afforded some refuge through protective measures or a current lack of economic incentive to exploit seahorses. The outer islands off Pattaya, including Ko Pai, and Ko Samaesan are areas with access managed, and presumably well-enforced, by the Thai Royal Navy (Navy Chart 001). Ko Lan and Ko Sak are not within the Navy protected area, but are both heavily visited by tourists year-round (Yeemin et al., 2009; Phillips, 2015), which may deter fishing activity in the area due to the importance of tourism. In contrast, no seahorses were observed in surveys at nearby Bang Saen within the same province, where seahorse markets were present, though survey sites had similar habitats as Pattaya and Samaesan. Because Pattaya is one of the prime beach resorts in Thailand, with tourism a major employer rather than fishing (Lertputtarak, 2012), there may be few buyers and low local demand for seahorses here. Thus, there is less of an incentive here to catch and sell seahorses as an income supplement, an example of “reducing the rewards” for wildlife trade (Pires and Moreto, 2011). Although, as seahorse prices rise (Laksanawimol et al., 2013), that trend might change, especially if tourism-based income goes down as well. Already we noted a shift in attitudes among our informal interview respondents, with fishers retaining seahorses from bycatch to sell instead of discarding them as they did previously.

For species of economic value, conservation goes beyond protecting good habitats, but also involves dealing with human behavior and economic drivers (Bennett et al., 2002; Brashares et al., 2011; Lotze et al., 2011; Challender and MacMillan, 2014). Protected area designs based on habitat quality will exclude species living in marginal environments (Linkie et al., 2007). For example, protected areas that are solely focused on healthy coral reefs or seagrass beds would miss the populations of *H. spinosissimus* off Chonburi province, which were mostly found in soft-bottom habitats with low topography. Not surprisingly, the establishment of marine protected areas (MPAs) in Australia and the Philippines did not lead to increased seahorse populations within the MPAs (Yasue et al., 2012; Harasti et al., 2014). However, proper pre-MPA evaluations and mapping should capture representative habitat diversity.

One conservation measure targeting behavior to mitigate wildlife trade is reducing consumer demand, with some success reported for the shark fin trade (Whitcraft et al., 2014; Eriksson and Clarke, 2015). Although access to market directly affects seahorse populations in Thailand, reducing demand for seahorses as traditional medicines is only a partial solution with most wild seahorses entering the trade from trawl bycatch (Perry et al., 2010; Laksanawimol et al., 2013). Similarly, shark conservation depends on decreasing bycatch levels through area closures or gear modifications as well as demand by consumers (Ward et al., 2008; Watson et al., 2009). Seahorse conservation efforts have to be predicated on alleviating overall fishing pressure, from artisanal fishing to trawling. On a smaller scale, artisanal fishers could be persuaded to release any seahorses caught, or to only keep seahorses >10 cm in height (Foster and Vincent, 2005). Thailand has several fisheries regulations already in place, but conversations with local community members indicate that enforcement of these restrictions may be an issue. Still, the Thai government recently enacted strict measures against illegal commercial fishing, grounding unregistered trawlers and banning illegal gear, affecting approximately 16,000 illegal vessels (Bangkok Post, 2015). While draconian, the hope is that these controls will eventually lead to the recovery of marine resources.

The fisheries-related issues we discuss here are not unique to Thailand, but a major challenge for Southeast Asia that go beyond seahorse species protection. Overfishing and destructive fishing pose the greatest threats to marine systems in the region (Burke et al., 2002; Loh and Jaafar, 2015). As seahorses illustrate, non-target species caught as bycatch may go unrecorded while wild populations become heavily impacted (Kumar and Deepthi, 2006). Addressing these biodiversity losses would require extensive fisheries regulation, policy action and enforcement of existing laws to protect natural resources.

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References

Alexiades, A., Fisher, W., 2015. Broad-scale habitat classification variables predict maximum local abundance for native but not non-native trout in New York streams. Aquat. Conserv. 25, 31–40.

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral. Ecol. 26, 32–46.

Aylesworth L., Loh T.-L., Rongrongmuang W. and Vincent A.C.J., Approaches to locating cryptic and data-poor marine fishes for conservation, (Unpublished results).

Aylesworth L., Phoonsawat R., Suvanachai P., Vincent A.C.J., Generating spatial data for marine conservation and management, Biodiv. Conserv., (in press).

Aylesworth, L., 2014. *Hippocampus kuda*. The IUCN Red List of Threatened Species. Version 2015.1.

Bailey, H., Thompson, P., 2009. Using marine mammal habitat modelling to identify priority conservation zones within a marine protected area. Mar. Ecol. Prog. Ser. 378, 279–287.

Bangkok Post, 2015. Fish Trade Dries up as Illegal Fleets Remain in Port. (Bangkok Post) http://www.bangkokpost.com/news/general/609712/fish-trade-dries-up-as-illegal-fleets-remain-in-port.

Baum, J.K., Vincent, A.C.J., 2005. Magnitude and inferred impacts of the seahorse trade in Latin America. Environ. Conserv. 32, 305–319.

Bell, E.M., Lockyear, J.F., McPherson, J.M., Marsden, A.D., Vincent, A.C.J., 2003. First field studies of an endangered South African seahorse, *Hippocampus capensis*. Environ. Biol. Fish 67, 35–46.

Bennett, E.L., Milner-Gulland, E.J., Bakarr, M., Eves, H.E., Robinson, J.G., Wilkie, D.S., 2002. Hunting the world's wildlife to extinction. Oryx 36, 328–329.

Blake, J.G., Mosquera, D., Loiselle, B.A., Swing, K., Guerra, J., Romo, D., 2016. Spatial and temporal activity patterns of ocelots *Leopardus pardalis* in lowland forest of eastern Ecuador. J. Mammal. 97, 455–463.

Brashares, J.S., Arcese, P., Sam, M.K., Coppolillo, P.B., Sinclair, A.R.E., Balmford, A., 2004. Bushmeat hunting, wildlife declines, and fish supply in West Africa. Science 306, 1180–1183.

Brashares, J.S., Golden, C.D., Weinbaum, K.Z., Barrett, C.B., Okello, G.V., 2011. Economic and geographic drivers of wildlife consumption in rural Africa. Proc. Natl. Acad. Sci. U. S. A. 108, 13931–13936.

Braunisch, V., Suchant, R., 2010. Predicting species distributions based on incomplete survey data: the trade-off between precision and scale. Ecography 33, 826–840.

Bulte, E.H., 2003. Open access harvesting of wildlife: the poaching pit and conservation of endangered species. Agric. Econ. 28, 27–37.

Burke, L., Selig, E., Spalding, M., 2002. Reefs at Risk in Southeast Asia. World Resources Institute, Washington DC.

Burke, L.M., Reytar, K., Spalding, M., Perry, A., 2011. Reefs at Risk Revisited. World Resources Institute, Washington DC.
Burton, M., 1999. An assessment of alternative methods of estimating the effect of the ivory trade ban on poaching effort. Ecol. Econ. 30, 93–106.
Caldwell, I.R., Vincent, A.C.J., 2012. Revisiting two sympatric European seahorse species: apparent decline in the absence of exploitation. Aquat. Conserv. Mar. Freshwat. Ecosyst. 435, 427–435.
Challender, D.W.S., MacMillan, D.C., 2014. Poaching is more than an enforcement problem. Conserv. Lett. 7, 484–494.
Choo, C.K., Liew, H.C., 2003. Spatial distribution, substrate assemblages and size composition of sea horses (Family Syngnathidae) in the coastal waters of Peninsular Malaysia. J. Mar. Biol. Assoc. UK 83, 271–276.
Choo, C., Liew, H., 2005. Exploitation and trade in seahorses in Peninsular Malaysia. Malay. Nat. J. 57, 57–66.
Clarke, S., Milner-Gulland, E., Bjørndal, T., 2007. Social, economic, and regulatory drivers of the shark fin trade. Mar. Resour. Econ. 22, 305–327.
Curtis, J., Vincent, A., 2005. Distribution of sympatric seahorse species along a gradient of habitat complexity in a seagrass-dominated community. Mar. Ecol. Prog. Ser. 291, 81–91.
Dias, T., Rosa, I., 2003. Habitat preferences of a seahorse species, *Hippocampus reidi* (Teleostei: Syngnathidae) in Brazil. Aqua Int. J. Ichthy. 6, 165–176.
Dixon, P., 2003. VEGAN, a package of R functions for community ecology. J. Veg. Sci. 14, 927–930.
Duarte, C.M., 2002. The future of seagrass meadows. Environ. Conserv. 29, 192–206.
Engler, M., Parry-Jones, R., 2007. Opportunity or Threat? The Role of the European Union in Global Wildlife Trade. TRAFFIC Europe, Brussels, Belgium.
Eriksson, H., Clarke, S., 2015. Chinese market responses to overexploitation of sharks and sea cucumbers. Biol. Conserv. 184, 163–173.
Ferrier, S., Powell, G.V.N., Richardson, K.S., et al., 2004. Mapping more of terrestrial biodiversity for global conservation assessment. Bioscience 54, 1101–1109.
Foster, S., Vincent, A., 2004. Life history and ecology of seahorses: implications for conservation and management. J. Fish Biol. 65, 1–61.
Foster, S.J., Vincent, A.C.J., 2005. Enhancing sustainability of the international trade in seahorses with a single minimum size limit. Conserv. Biol. 19, 1044–1050.
Foster, S., Wiswedel, S., Vincent, A., 2016. Opportunities and challenges for analysis of wildlife trade using CITES data - seahorses as a case study. Aquat. Conserv. 26, 154–172.
Gaston, K.J., Fuller, R.A., 2007. Biodiversity and extinction: losing the common and the widespread. Prog. Phys. Geogr. 31, 213–225.
Gaston, K.J., Fuller, R.A., 2008. Commonness, population depletion and conservation biology. Trends Ecol. Evol. 23, 14–19.
Giles, B.G., Ky, T.S., Hoang, D.H., Vincent, A.C.J., 2006. The catch and trade of seahorses in Vietnam. Biodivers. Conserv. 15, 2497–2513.
Godfrey, E., Sanders, G., 2004. Effect of water hardness on oocyte quality and embryo development in the African clawed frog (*Xenopus laevis*). Comp. Med. 54, 170–175.
Gristina, M., Cardone, F., Carlucci, R., Castellano, L., Passarelli, S., Corriero, G., 2015. Abundance, distribution and habitat preference of *Hippocampus guttulatus* and *Hippocampus hippocampus* in a semi-enclosed central Mediterranean marine area. Mar. Ecol. 36, 57–66.
Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. Ecol. Model. 135, 147–186.
Harasti, D., 2016. Declining seahorse populations linked to loss of essential marine habitats. Mar. Ecol. Prog. Ser. 546, 173–181.
Harasti, D., Martin-Smith, K., Gladstone, W., 2014. Does a no-take marine protected area benefit seahorses? PLoS One 9, e105462.
Hill, J.M., Diefenbach, D.R., 2014. Occupancy patterns of regionally declining grassland sparrow populations in a forested Pennsylvania landscape. Conserv. Biol. 28, 735–744.
Hothorn, T., Hornik, K., Zeileis, A., 2006. Unbiased recursive partitioning: A conditional inference framework. J. Comput. Graph. Stat. 15, 651–674.
Issaris, Y., Katsanevakis, S., 2010. Non-destructive distance sampling surveys for population density and abundance estimations of benthic fauna. 39th CIESM Congress Proceedings 548. CIESM, Venice.
James, P.L., Heck, K.L., 1994. The effects of habitat complexity and light intensity on ambush predation within a simulated seagrass habitat. J. Exp. Mar. Biol. Ecol. 176, 187–200.
Kumar, A.B., Deepthi, G.R., 2006. Trawling and by-catch : implications on marine ecosystem. Curr. Sci. India 90, 922–931.
Laksanawimol, P., Petpiroon, S., Damrongphol, P., 2013. Trade of seahorses, *Hippocampus* spp. (Actinopterygii: Syngnathiformes: Syngnathidae), on the east coast of the Gulf of Thailand. Acta Ichthyol. Piscat. 43, 229–235.
Landi, A.A., Vokoun, J.C., Howell, P., Auster, P., 2014. Predicting use of habitat patches by spawning horseshoe crabs (*Limulus polyphemus*) along a complex coastline with field surveys and geospatial analyses. Aquat. Conserv. (Early View).
Lawson, J.M., Foster, S.J., Lim, A.C.O., Chong, V.C., Vincent, A.J., 2015. Novel life-history data for threatened seahorses provide insight into fishery effects. J. Fish Biol. 86, 1–15.
Lertputtarak, S., 2012. The relationship between destination image, food image, and revisiting Pattaya, Thailand. J. Bus. Manag. 7, 111–122.
Lim, A., Chong, V., Wong, C., Choo, C., 2011. Diversity, habitats and conservation threats of syngnathid (Syngnathidae) fishes in Malaysia. Trop. Zool. 24, 193–222.
Lin, Q., Lu, J., Gao, Y., Shen, L., Cai, J., Luo, J., 2006. The effect of temperature on gonad, embryonic development and survival rate of juvenile seahorses, *Hippocampus kuda* Bleeker. Aquaculture 254, 701–713.
Linkie, M., Dinata, Y., Nugroho, A., Haidir, I.A., 2007. Estimating occupancy of a data deficient mammalian species living in tropical rainforests: sun bears in the Kerinci Seblat region, Sumatra. Biol. Conserv. 137, 20–27.
Loh, T.-L., Jaafar, Z., 2015. Turning the tide on bottom trawling. Aquat. Conserv. 25, 581–583.
Lotze, H.K., Coll, M., Magera, A.M., Ward-Paige, C., Airoldi, L., 2011. Recovery of marine animal populations and ecosystems. Trends Ecol. Evol. 26, 595–605.
Lourie, S.A., Pritchard, J.C., Casey, S.P., Truong, S.K., Hall, H.J., Vincent, A.C.J., 1999. The taxonomy of Vietnam's exploited seahorses (family Syngnathidae). Biol. J. Linn. Soc. 66, 231–256.
Lourie, S.A., Foster, S., Cooper, E., Vincent, A.C.J., 2004. A Guide to the Identification of Seahorses. Project Seahorse and TRAFFIC North America, Washington DC.
Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., Hornik, K., 2015. Cluster: Cluster Analysis Basics and Extensions. R Package Version 2.0.2.
Marcus, J.E., Samoilys, M.A., Meeuwig, J.J., Villongco, Z.A.D., Vincent, A.C.J., 2007. Benthic status of near-shore fishing grounds in the central Philippines and associated seahorse densities. Mar. Pollut. Bull. 54, 1483–1494.
Miller, S.L., Botzler, R.G., 1995. Recovery of *Pasteurella multocida* from experimentally-exposed freshwater snails. J. Wildl. Dis. 31, 358–363.
Moreau, M.-A., Vincent, A.C.J., 2004. Social structure and space use in a wild population of the Australian short-headed seahorse *Hippocampus breviceps* Peters, 1869. Mar. Freshw. Res. 55, 231.
Murugan, A., Dhanya, S., Rajagopal, S., Balasubramanian, T., 2008. Seahorses and pipefishes of the Tamil Nadu coast. Curr. Sci. India 95, 253–260.
Nijman, V., 2009. An overview of international wildlife trade from Southeast Asia. Biodivers. Conserv. 19, 1101–1114.
Panithanarak, T., Karuwancharoen, R., Na-Nakorn, U., Nguyen, T.T., 2010. Population genetics of the spotted seahorse (*Hippocampus kuda*) in Thai waters: Implications for conservation. Zool. Stud. 49, 564–576.
Pavoine, S., Vallet, J., Dufour, A.-B., Gachet, S., Daniel, H., 2009. On the challenge of treating various types of variables: application for improving the measurement of functional diversity. Oikos 118, 391–402.
Perante, N., Pajaro, M.G., Meeuwig, J.J., Vincent, A.C.J., 2002. Biology of a seahorse species, *Hippocampus comes* in the central Philippines. J. Fish Biol. 60, 821–837.
Peres-Neto, P.R., Jackson, D.A., Somers, K.M., 2008. Giving meaningful interpretation to ordination axes: assessing loading significance in principal component analysis. Ecology 84, 2347–2363.
Perry, A.L., Lunn, K.E., Vincent, A.C.J., 2010. Fisheries, large-scale trade, and conservation of seahorses in Malaysia and Thailand. Aquat. Conserv. 20, 464–475.
Phillips, W., 2015. Tourism threats to coral reef resilience at Koh Sak, Pattaya Bay. Environ. Nat. Res. J. 13, 47–60.
Pimm, S.L., Jenkins, C.N., Abell, R., et al., 2014. The biodiversity of species and their rates of extinction, distribution, and protection. Science 344, 1246752.
Pires, S.F., Moreto, W.D., 2011. Preventing wildlife crimes: Solutions that can overcome the "Tragedy of the Commons.". Eur. J. Crim. Policy Res. 17, 101–123.
Project Seahorse, 2003. Hippocampus trimaculatus. The IUCN Red List of Threatened Species Version 2015.1.
Purcell, S.W., Clarke, K.R., Rushworth, K., Dalton, S.J., 2014. Defining critical habitats of threatened and endemic reef fishes with a multivariate approach. Conserv. Biol. 28, 1688–1698.
Reddy, S.M.W., Wentz, A., Aburto-Oropeza, O., Maxey, M., Nagavarapu, S., Leslie, H.M., 2013. Evidence of market-driven size-selective fishing and the mediating effects of biological and institutional factors. Ecol. Appl. 23, 726–741.
Rosa, I.L., Sampaio, C.L.S., Barros, A.T., 2006. Collaborative monitoring of the ornamental trade of seahorses and pipefishes (Teleostei: Syngnathidae) in Brazil: Bahia State as a case study. Neotrop. Ichthyol. 4, 247–252.
Rosa, I., Oliveira, T., Castro, A., 2007. Population characteristics, space use and habitat associations of the seahorse *Hippocampus reidi* (Teleostei: Syngnathidae). Neotrop. Ichthyol. 5, 405–414.
Rosen, G.E., Smith, K.F., 2010. Summarizing the evidence on the international trade in illegal wildlife. EcoHealth 7, 24–32.
Schultz, P.W., 2011. Conservation means behavior. Conserv. Biol. 25, 1080–1083.
Sheng, J., Lin, Q., Chen, Q., Gao, Y., Shen, L., Lu, J., 2006. Effects of food, temperature and light intensity on the feeding behavior of three-spot juvenile seahorses, *Hippocampus trimaculatus* Leach. Aquaculture 256, 596–607.
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. Aquat. Conserv. 19, 588–595.
Stallings, C.D., 2009. Fishery-independent data reveal negative effect of human population density on Caribbean predatory fish communities. PLoS One 4, e5333.
Teske, P.R., Hamilton, H., Matthee, C.A., Barker, N.P., 2007. Signatures of seaway closures and founder dispersal in the phylogeny of a circumglobally distributed seahorse lineage. BMC Evol. Biol. 7, 138.
Vincent, A.C.J., Foster, S.J., Koldewey, H.J., 2011. Conservation and management of seahorses and other Syngnathidae. J. Fish Biol. 78, 1681–1724.
Walsh, P.D., Abernethy, K.A., Bermejo, M., et al., 2003. Catastrophic ape decline in western equatorial Africa. Nature 422, 611–614.
Ward, P., Lawrence, E., Darbyshire, R., Hindmarsh, S., 2008. Large-scale experiment shows that nylon leaders reduce shark bycatch and benefit pelagic longline fishers. Fish. Res. 90, 100–108.
Watson, J.T., Essington, T.E., Lennert-Cody, C.E., Hall, M.A., 2009. Trade-offs in the design of fishery closures: management of silky shark bycatch in the eastern Pacific Ocean tuna fishery. Conserv. Biol. 23, 626–635.
Wessels, K., 1999. The use of land facets as biodiversity surrogates during reserve selection at a local scale. Biol. Conserv. 89, 21–38.

Whitcraft, S., Hofford, A., Hilton, P., O'Malley, M., Jaiteh, V., Knights, P., 2014. Evidence of Declines in Shark Fin Demand, China. WildAid, San Francisco, CA.
Williams, G.J., Gove, J.M., Eynaud, Y., Zgliczynski, B.J., Sandin, S.A., 2015. Local human impacts decouple natural biophysical relationships on Pacific coral reefs. Ecography 38, 751–761.
Wiswedel, S., 2012a. *Hippocampus spinosissimus*. The IUCN Red List of Threatened Species. Version 2015.1.
Wiswedel, S., 2012b. *Hippocampus kelloggi*. The IUCN Red List of Threatened Species. Version 2015.1.
Yasue, M., Nellas, A., Vincent, A.C.J., 2012. Seahorses helped drive creation of marine protected areas, so what did these protected areas do for the seahorses? Environ. Conserv. 39, 183–193.
Yeemin, T., Saenghaisuk, C., Sutthacheep, M., Pengsakun, S., Klinthong, W., Saengmanee, K., 2009. Conditions of coral communities in the Gulf of Thailand: a decade after the 1998 severe bleaching event. Galaxea 11, 207–217.