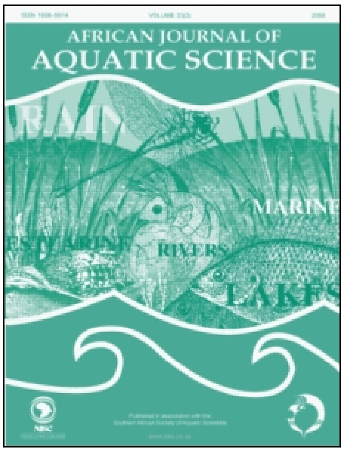

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The distribution and abundance of the endangered Knysna seahorse *Hippocampus capensis* (Pisces: Syngnathidae) in South African estuaries

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The occurrence, distribution and abundance of the endangered Knysna seahorse *Hippocampus capen*sis in 10 estuaries on South Africa's warm temperate south coast, were investigated. Seahorses were found only in the Knysna, Swartvlei and Keurbooms estuaries. Sex ratios were even and, in most cases, more adults were found than juveniles. During the first year of study, seahorse densities were higher in the Swartvlei and Keurbooms estuaries than in the comparatively larger Knysna Estuary but, during the second year, seahorses were absent from the Keurbooms estuary, and the population size in the Swartvlei Estuary had decreased by more than 80%. These results suggest that, although the two smaller estuaries are able to support comparatively high densities of seahorses, population sizes may fluctuate considerably. Population size estimates for the Knysna Estuary were similar to those obtained in a previous study, suggesting that this estuary may represent a more stable environment and may thus be particularly important for the survival and conservation of this species.

Keywords: freshwater floods, Keurbooms Estuary, Knysna Estuary, Swartvlei Estuary, patchy distribution, population size fluctuation, submerged vegetation

Introduction

The Knysna seahorse *Hippocampus capensis* Boulenger, 1900 was the first seahorse species listed as endangered on the IUCN Red List (Hilton-Taylor 2000) because of its limited distribution range, small population size and vulnerability to natural and anthropogenic disturbances. Despite its conservation status, little information is available on its population sizes, population structure and habitat preferences (Skelton 1987). Most studies on this species have been conducted under captive conditions (Fourie 1997, Lockyear *et al.* 1997, Tops 1999, Le Cheminant 2000), or have employed genetic methods (Toeffie 2000, Teske *et al.* 2003, 2005), except for an *in situ* ecological study of its abundance and distribution by Bell *et al.* (2003).

The Knysna seahorse is endemic to South Africa and has been recorded in the Knysna, Swartvlei and Keurbooms estuaries (Kok 1981, Whitfield 1989, Russell 1994, Figure 1). Anecdotal reports suggest that the species may also occur in the Klein Brak, Breede, Duiwenhoks and Goukou estuaries (Grange pers. comm.). It has never been reported in samples collected outside estuaries. Knysna seahorses are usually found in shallow water in association with aquatic vegetation (Bell *et al.* 2003) where its prehensile tail is used to grasp plants and other objects (Whitfield 1995). Previous studies indicated that the distribution of seahorses within the Knysna Estuary was patchy (Bell *et al.* 2003), and that large areas of habitat in this estuarine system may be unsuitable for *H. capensis* because of the absence of submerged vegetation (Toeffie 2000).

Construction developments are increasing along the species' available habitats (Skelton 1987), a recent example being the construction of a marina on Thesen's Island in the Knysna Estuary (Figure 2a). The associated domestic, industrial and recreational activities, as well as pollution events and other disturbances, may impact negatively on the seahorse populations (Skelton 1987). Apart from human activities, the seahorses are also threatened by freshwater floods. In the Swartvlei Estuary, for example, the breaching of the sand bar, which periodically separates this estuary from the sea resulted in a mass mortality that killed at least 3 000 seahorses. Seahorses inhabiting the shallow vegetated areas of the estuary were affected by the sudden drop in water level and were believed to have died as a result of high temperature (Russell 1994).

In the light of these potentially adverse impacts on the seahorse populations, research on *H. capensis* was required to suggest a management plan for the conservation of this endangered species. Here we present the results of a survey that continued some of the work reported by Bell *et al.* (2003). The main aims were to determine the estuaries in which Knysna seahorses occur and to describe their distribution and abundance within these systems. This information may be useful for identifying

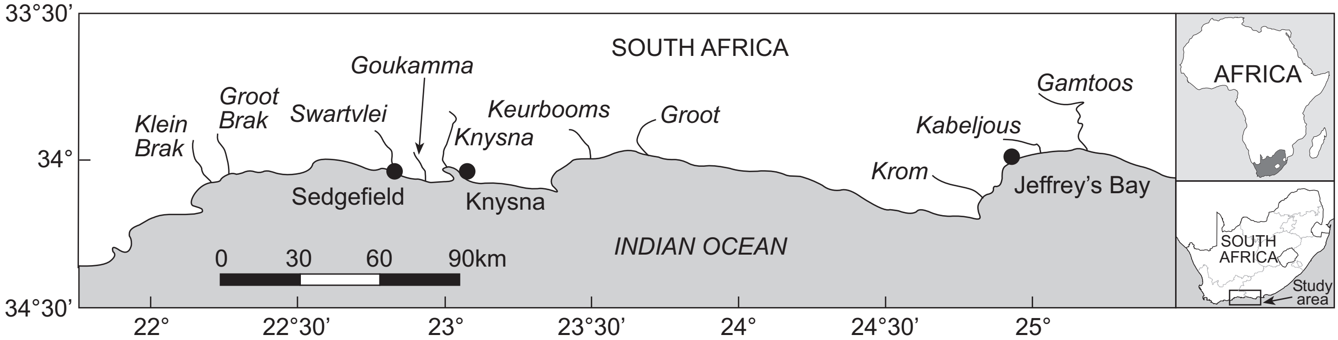

Figure 1: Map of the southern Cape coast showing estuaries sampled for seahorses

areas of high conservation value, where human activities should be managed accordingly. We also quantified seahorse population structures in the Knysna, Swartvlei and Keurbooms estuaries and estimated population sizes to provide a baseline for monitoring future changes in population size and composition.

Materials and methods

Estuaries studied

The Knysna, Swartvlei and Keurbooms estuaries (Figure 1) were sampled during 2001–2003 (Tables 1a and b). In addition, to determine the extent of the distribution of *Hippocampus capensis,* seven additional estuaries on South Africa's south coast (Figure 1) were surveyed between March and May 2002 (Table 1).

The Knysna Estuary, which was sampled over a period of 10 months, is the largest of the three systems in which *H. capensis* had previously been recorded. It can be divided into three major regimes: the mouth area represents the marine-dominated 'bay regime', the middle section represents the 'lagoonal regime' and the upper estuary represents the 'estuarine regime' (Largier *et al.* 2000). To determine the suitability of the different portions of the Knysna Estuary to provide habitat for *H. capensis*, the estuary was divided into six sampling areas (A–F, Figure 2a), each of which could be assigned to one of the three estuarine regimes: Area A represents the marine-dominated 'bay regime', areas B–E correspond to the 'lagoon regime', and area F represents the 'estuarine regime'. Environmental characteristics, including long-term salinity regimes, temperatures and approximate distributions of dominant organisms (used to divide the lagoon regime into four biologically meaningful units) within each of the six sampling areas, are listed in Table 2.

In comparison to the Knysna Estuary, the two smaller estuarine systems in which *H. capensis* has been recorded, the Swartvlei and Keurbooms estuaries, are characterised by more homogeneous environmental conditions: both are characterised by shallow water and have seagrass beds along their entire lengths (Whitfield *et al.* 1983, Duvenage and Morant 1984). Because of this and their comparatively smaller size, the Swartvlei and Keurbooms estuaries were not subdivided into sampling areas. Both estuaries were sampled twice (Table 1b). Spot surveys were performed on a number of other estuaries in the region (Klein Brak, Groot Brak, Goukamma, Groot, Kromme, Kabeljous and Gamtoos: Figure 1) to determine the extent of the distribution of *H. capensis*. All of these estuaries are located in the warm temperate coastal province (Day 1981) and, with the exception of the Kromme and the Gamtoos estuaries, they may close temporarily during times of low freshwater inflow.

Population size estimations

The surface area of each of the six sampling areas within the Knysna Estuary was estimated using an orthophoto map divided into 1 sec^2 geographical grid squares (approximately 8.3m^2). Aerial photographs were used to identify areas not inundated at spring low tide, which were excluded from surface area estimations because they are unlikely to provide habitat for seahorses. Surface areas of the Swartvlei (closed phase) and Keurbooms estuaries were determined using digital topographical data provided by the Chief Director: Surveys and Mapping, South Africa. In the case of the tidal Keurbooms Estuary, the areas located above the spring low tide mark (e.g. sandbanks, mudflats and islands) were subtracted from the total surface area. Seahorse abundance in each of the six sampling areas within the Knysna Estuary, and in the Swartlvlei and Keurbooms estuaries, was estimated by determining seahorse densities during surveys (see below). Seahorse density estimates were converted to individuals m^{-2} and then multiplied by the corresponding surface area estimates.

Sampling procedure

Visual transect surveys

In the Knysna Estuary, distribution and abundance of *Hippocampus capensis* were mostly determined by visual transect line counts using SCUBA, after Curtis *et al.* (2004). Grid squares were randomly selected and at least one site was sampled in each. The starting position and compass direction of each transect within a grid square were randomly selected and entered into a Garmin Etrex handheld GPS. On reaching a selected GPS position by boat, the anchor was released, and a diving reel was attached to it. Two divers were deployed and each searched for seahorses within 1m on either side of a 30m transect line while reeling it out along the predetermined compass direction.

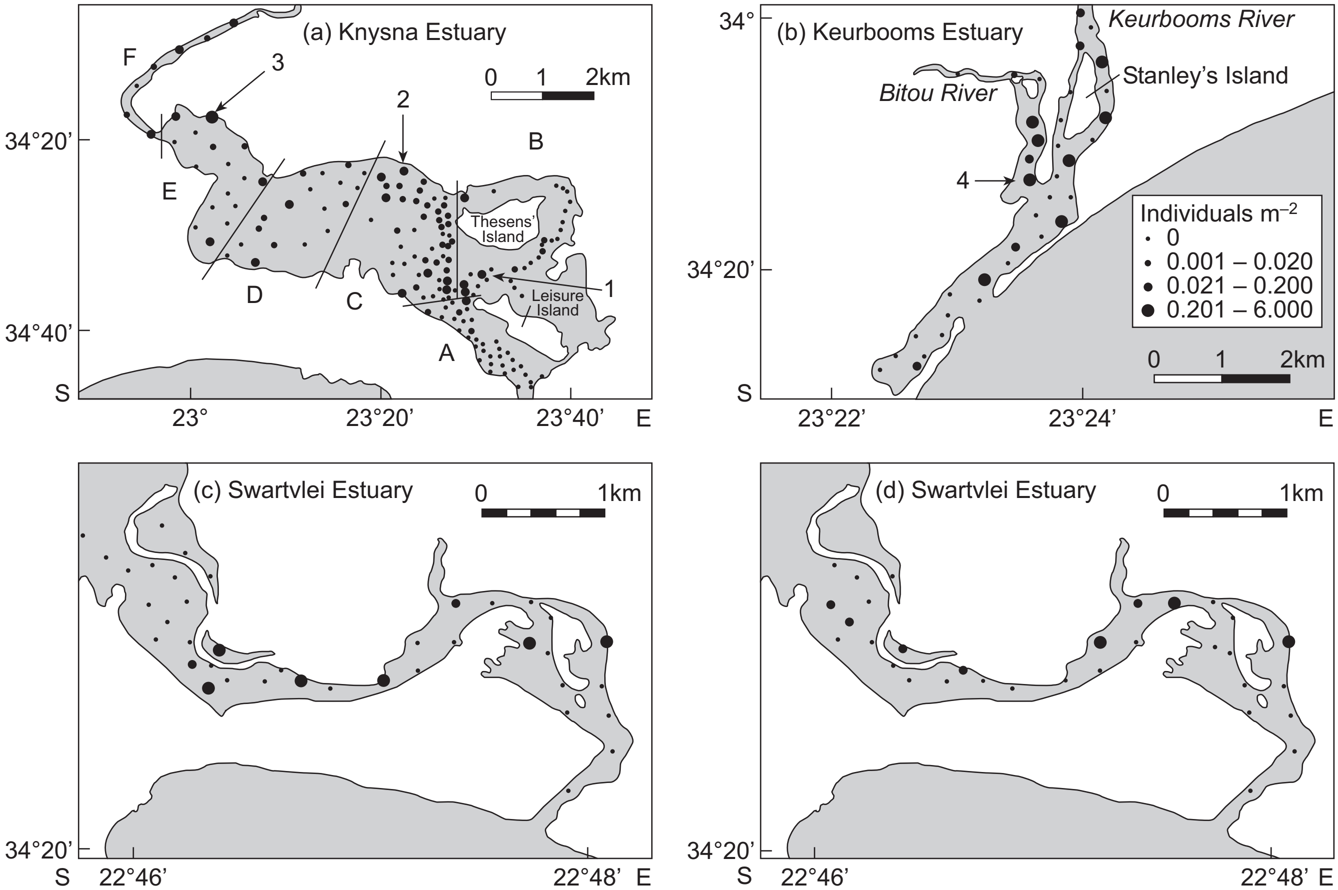

Figure 2: Maps of the three estuaries in which Knysna seahorses, *Hippocampus capensis*, were found: (a) Knysna, indicating sampling areas A–F; (b) Keurbooms (first sampling survey); (c) Swartvlei (first sampling survey); (d) Swartvlei (second sampling survey). The locations of four sites characterised by particularly high seahorse densities in the Knysna and Keurbooms estuaries are indicated (see Discussion for details). Grey shading indicates submerged areas and unshaded areas indicate dry land.

Table 1: Estuaries surveyed during this study, with survey dates and the number of sites sampled; Group (a) sampling sites were selected randomly and comprised a combination of visual census using SCUBA, and pushnet sampling; Group (b) sampling sites were selected randomly and pushnet sampling was used exclusively (both estuaries were sampled twice at approximately the same sites); Group (c) exploratory searches were performed to establish whether or not seahorses were present. Sampling sites were selected in relation to the presence of submerged vegetation

Estuary surveyed	Survey periods	No. of sampling sites
(a) Knysna	January 15–December 15, 2001	155
(b) Swartvlei (first survey)	January 15–February 15, 2002	32
Swartvlei (second survey)	December 15, 2002–January 15, 2003	32
Keurbooms (first survey)	March 8–April 10, 2002	38
Keurbooms (second survey)	March 8–April 10, 2003	38
Klein Brak	June 15–June 30, 2002	35
Groot Brak	July 15–July 30, 2002	35
Goukamma	April 17–April 25, 2002	25
Groot	October 15–October 20, 2002	20
Kromme	April 26–April 30, 2002	20
Kabeljous	May 1–May 3, 2002	20
Gamtoos	September 10–September 18, 2002	50

Table 2: Physical characteristics of sampling areas A–F within the Knysna Estuary. Size of the sampling areas was based on both abiotic environmental conditions (e.g. salinity regime and currents as described in Largier *et al*. (2000)) and biotic conditions (distribution limits of common estuarine animals and dominant aquatic plants established in this study)

Area	Description	Environmental conditions
A	Mouth area	High current velocity; salinity usually >34 ppt; submerged vegetation covering <1% of area; dominant plant: *Zostera capensis*
B	Ashmead channel	Area surrounding Thesen's Island; salinity 30–34 ppt; dominant plant: *Zostera capensis*
C	Lagoon (lower reaches)	Salinity 30–34 ppt; upper distribution limit of the spiny starfish, *Marthasteria glacialis*; dominant plant: *Caulerpa filiformis*
D	Lagoon (middle reaches)	Salinity 30–34 ppt; dominant plant: *Codium extricatum*
E	Lagoon (upper reaches)	Salinity 30–34 ppt; upper distribution limit of the shaggy seahare, *Bursatella leachi*
F	Upper estuary	Salinity <30 ppt; reduced tidal influence; high turbidity; dominant plant: *Ruppia cirrhosa*

Pushnet sampling

Visual searching was impractical in areas of very dense vegetation (approximately 60% vegetation cover or more), as it became difficult for the divers to detect seahorses due to insufficient light penetration and to the release of fine silt when the vegetation was disturbed. The method thus had to be adjusted to local environmental conditions. The divers attempted to detect seahorses by touch but, when this also proved impractical, it was eventually decided to sample seahorses by collecting vegetation with a pushnet. The pushnet comprised a 1m x 1m metal frame that served as an opening and which was held in a vertical position (with a 20cm rake structure attached underneath this) which was pushed into the substrate below the root system of the vegetation to dislodge it without harming any seahorses it contained, and a 5mm mesh 1.5m long bag. The pushnet was moved along the transect line over a distance of 10m (i.e. covering 10m^2), in increments of between 1m and 3m depending on the weight of the dislodged vegetation. Blades of seagrass that protruded beyond the edge of the net mouth were pushed back towards the centre by each diver to prevent seahorses from escaping. Then, on the deck of the boat or in shallow water, the vegetation was teased apart and captured seahorses were counted. It is unlikely that a significant number of seahorses escaped while these samples were collected because, when disturbed, they tended to continue grasping their holdfasts. No mortalities were reported, and seahorses were subsequently returned to the sampling site.

Sampling effort

In the Knysna Estuary a total of 155 sites were sampled with two to four transect surveys being performed at each, resulting in a total of 583 transect surveys. The pushnet was used at 17 sites. At several sampling sites, both visual assessments and pushnet sampling were performed, depending on the density of vegetation. The total number of pushnet transects done in the Knysna Estuary was 22. Due to the high density of submerged vegetation in the Swartvlei and Keurbooms estuaries only the pushnet method was used here. In both years in which these two estuaries were sampled a total of 32 (Swartvlei) and 41 (Keurbooms) pushnet transects were taken. GIS coordinates of the randomly-selected sites that were sampled in these estuaries during the first year were recorded, and sampling during the second year took place at approximately the same localities.

A combination of underwater visual assessment and pushnet sampling was used to survey the Klein Brak, Groot Brak, Goukamma, Groot, Kromme, Kabeljous and Gamtoos estuaries, with between 20 and 50 sites being sampled in each, depending on its size (Table 1c). The total area surveyed at each sampling site in these estuaries ranged from 10–100m^2. As these exploratory searches were aimed at determining whether seahorses were present in these systems, they focused on areas characterised by vegetation stands, as these were the most likely localities where seahorses were expected to be found (Bell *et al.* 2003).

Seahorse densities

Seahorse densities at individual sites within the different regions of the Knysna Estuary, and within the two smaller estuaries, were plotted onto GIS maps. Ninety-five percent confidence intervals of mean density values were estimated by resampling the data-sets comprising seahorse densities at each site with replacement (100 000 bootstrap replications) using the program PopTools Version 2.6.2 (Hood 2004).

Two data-sets comprising mean population density data were analysed: the first consisted of density data from each of the six sampling areas in the Knysna Estuary, and the second comprised combined data from these sampling areas, as well as density data from the Swartvlei and Keurbooms estuaries. Residuals were not normally distributed and the data sets were characterised by a high proportion of zeros, which made it difficult to justify the application of both parametric and non-parametric statistical tests. Manley (1997) recommended that in such cases, tests be carried out on re-sampled data. To compare seahorse densities in sampling areas and estuaries, we determined means and 95% confidence intervals using 100 000 bootstrap replications generated with PopTools and then determined whether the differences were significant by using t-tests for two independent samples on randomly resampled data (100 000 replications), using the program Resampling, Version 1.3 (Howell 2001). As approximately the same sites in the Swartvlei estuary were sampled in the first and second surveys, a t-test on paired samples was used in this case.

Population structure

To determine whether male, female and juvenile seahorses were spatially separated in the Knysna Estuary, and whether the ratios of these differed between the three estuaries, it was attempted to determine the sex of each

Table 3: Estimates of surface area, seahorse density and seahorse abundance in the Knysna, Swartvlei and Keurbooms estuaries. Estimates from the Knysna Estuary were from six sampling sites (sites A-F, Figure 1). Estimates from Swartvlei and Keurbooms estuaries were each based on two sampling surveys (see Table 1 for details). The Swartvlei and Keurbooms estuaries were both sampled twice. Ninety-five percent confidence intervals of seahorse abundance were obtained using 10 000 bootstrap replications

Estuary	Sampling area/survey	Surface area (m^2)	No. of seahorses	Seahorse density (individuals m^{-2})	Seahorse abundance (no. of individuals) and 95% confidence intervals (in brackets)
Knysna	A	840 463	5	0.00	
	B	290 574	55	0.01	
	C	1 204 026	94	0.01	
	D	1 173 797	46	0.01	
	E	1 480 493	50	0.65	
	F	420 475	29	0.14	
	A–F combined	5 409 828	279	0.01	62 120 (41 142–81 607)
Swartvlei	Survey 1	3 823 771	57	0.26	994 085 (392 712–1 674 192)
	Survey 2	3 823 771	14	0.04	175 845 (82 741–279 251)
Keurbooms	Survey 1	3 020 441	102	0.28	836 298 (241 635–1 706 549)
	Survey 2	3 020 441	0	0.00	0 (0)

seahorse encountered. It is difficult to distinguish between juvenile and adult female seahorses, because secondary sexual characteristics are not obvious. Adult males, on the other hand, are easily identified by the presence of a brood pouch, which was recorded in individuals having a standard length (Lourie 2003) of 4cm or larger. Individuals that lacked a brood pouch were thus recorded as females — if their standard length was 4cm or larger — or as juveniles if it was less than 4cm. Percentages of the numbers of male, female and juvenile seahorses present within each area or estuary were compared in a pair-wise fashion using the log-likelihood ratio goodness-of-fit test (Sokal and Rohlf 1995). It was necessary to use percentages rather than actual numbers of seahorses, because of differences in the number of transects per site.

Results

Seahorse distributions

Seahorses were recorded only in the Knysna, Keurbooms and Swartvlei estuaries (Table 3), and many sampling sites in all three estuaries contained no seahorses (Figure 2). At least one seahorse was found in 41% of the sites (64 out of 155) in the Knysna Estuary, 25% (8 out of 32 sites) in the Swartvlei Estuary (in both the first and second surveys) and 32% (14 out of 41 sites) in the Keurbooms Estuary (first survey). No seahorses were recorded during the second survey of the Keurbooms Estuary.

Seahorse densities and population size estimates

In the Knysna Estuary, mean seahorse densities did not differ significantly between most of the six sampling areas (Figure 3a). Significant differences in mean density were found only between area A and all other areas and between areas C and E (Table 4a). No seahorses were found in 87% of the sites in area A, compared to none in 52% of all remaining Knysna Estuary sites combined. Seahorse density and population size estimates were higher in the Swartvlei (both surveys) and Keurbooms (first survey) estuaries than in the Knysna Estuary (Figure 3b and Table

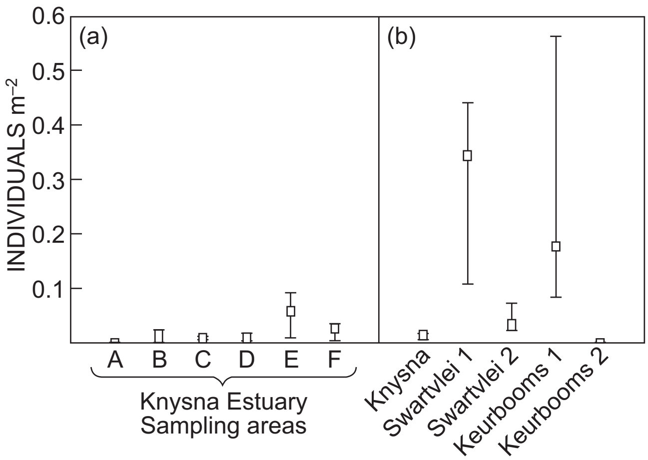

Figure 3: Seahorse densities at (a) sampling areas A–F within the Knysna Estuary and (b) in the three estuaries sampled (including data from two surveys each of the Swartvlei and Keurbooms estuaries). Squares represent means and bars are 95% confidence intervals obtained from bootstrapped data

4b, respectively). The difference in mean seahorse density was significant between the datasets of the first surveys of the Swartvlei and Keurbooms estuaries and that of the Knysna Estuary ($P < 0.01$; Table 4b).

Seahorses were particularly abundant at four sites (Figures 2a, 2c). These included one in area B located between the two islands in the Knysna Estuary (0.19 seahorses m^{-2}); (2) one in area C (0.22 seahorses m^{-2}), one in area E in the upper reaches of the Knysna Estuary (0.33 seahorses m^{-2}) (Figure 2a), and one at the confluence of the Bitou River and the Keurbooms Estuary (Figure 2c; 6 seahorses m^{-2}).

Population structure

In the Knysna Estuary there was a significant difference in sex ratio in sampling areas A to F ($G = 97.38$, $P < 0.01$) (Table 5). However, when area A — where only four adult

Table 4: Student's t statistics (above diagonal) and P values (below diagonal) of t-tests on randomised *Hippocampus capensis* abundance data (individuals m^{-2}); (a) pairwise comparisons among the six sampling areas within the Knysna Estuary; (b) pairwise comparisons among the three estuaries inhabited by *H. capensis*, including data from two surveys of the Swartvlei Estuary. Significance of tests is indicated as follows: NS = not significant; * P < 0.05; **P < 0.01

		A	B	C	D	E	F
(a)	A	–	1.6	4.0	3.0	2.6	3.3
	B	*	–	0.5	0.1	1.9	0.5
	C	**	NS	–	0.6	2.8	1.6
	D	**	NS	NS	–	1.6	0.8
	E	**	NS	**	NS	–	0.8
	F	**	NS	NS	NS	NS	–

(b)	1 Knysna	2 Swartvlei (first survey)	3 Swartvlei (second survey)	4 Keurbooms (first survey)
1	–	5.0	3.5	3.4
2	**	–	0.8	0.1
3	**	NS	–	1.4
4	**	NS	NS	–

females and no adult males were found — was excluded from the analysis, there was no significant difference (G = 0.47, P = 0.98), indicating that sex ratios were even. Adults outnumbered juveniles in all sampling areas in the Knysna Estuary (G = 20.69, P < 0.01 (area A included); G = 16.91, P < 0.01 (area A excluded)). Relative proportions of adult and juvenile seahorses were similar in the three estuaries during the first surveys (G = 5.71, P = 0.06). However, during the second Swartvlei survey no males were found, and juveniles outnumbered adults.

Discussion

Seahorse density

The mean density of seahorses in the Knysna Estuary (0.0114 individuals m^{-2}) was slightly higher than the value of 0.0089 individuals m^{-2} previously found by Bell *et al.* (2003). Sampling effort differed between the two studies: almost twice as many sites were sampled in the present study, and more than one transect survey was conducted at each site. Moreover, pushnet sampling was employed so as to sample those areas characterised by dense vegetation more effectively. The similar results may, nonetheless, be an indication that the population size in the Knysna Estuary fluctuates comparatively less than those in the two smaller estuaries.

Seahorse distributions

Seahorses were found throughout all three estuaries, except in the mouth area of the Knysna Estuary. The fact that the remaining areas in the Knysna Estuary are characterised by considerable differences in long-term environmental parameters such as temperature and salinity (Largier *et al.* 2000) suggests that Knysna seahorses can tolerate a wide range of environmental conditions, and that their distributions are not strongly affected by them. This is supported by laboratory studies by Lockyear *et al.* (1997), who found that *Hippocampus capensis* tolerated temperatures ranging from 14–28°C over a period of three months, and by Riley (1986) who reported that Knysna seahorses could tolerate salinities ranging from 1–59ppt. Moreover, Knysna seahorses reproduced in water of salinities between 20 and 25ppt (Lockyear *et al.* 1997) and at approximately 35 ppt (M Gunter, Port Nolloth Sea Farms, pers. comm.) over several generations, which indicates that the high salinity in the mouth area of the Knysna Estuary is not the factor responsible for the absence of seahorses there.

The presence of seahorses near the head of the Knysna Estuary, which is characterised by low salinity and high turbidity (Largier *et al.* 2000), suggests that *Hippocampus capensis* is an estuarine-dependent species. As estuarine-dependent species are well adapted to environmental fluctuations and extremes, their distribution may be limited by environmental factors other than salinity and temperature (Boesch 1977, Teske and Wooldridge 2004). For example, in South African estuarine systems *Atherina breviceps* are primarily associated with aquatic macrophyte beds rather than with a particular salinity regime (Ter Morshuizen and Whitfield 1994), and the Australian goby *Pseudogobius olorum* was reported to occur specifically in those regions of estuaries characterised by a high silt component (Gill and Potter 1993, Young *et al.* 1997). Most seahorses recorded during this study (viz. 96%) were associated with a plant holdfast, whereas 2% were associated with invertebrates such as sponges and ascidians, and 2% were not grasping any holdfast when recorded. The main reason for the low seahorse density near the Knysna Estuary's mouth area may thus be low vegetation cover, although strong currents in this portion of the estuary may also play a role, as most species living in estuaries prefer calm water (Day 1981).

Population structure

Males and females were not spatially separated in the Knysna Estuary and equal sex ratios were found at most sampling sites, although departures from this trend were observed when sample sizes were small. The unbiased sex ratios found in this study are consistent with the results of Bell *et al.* (2001). The lower proportion of juveniles found at most sites is also consistent with other studies on seahorse

Table 5: Numbers and percentages of male, female and juvenile seahorses found in six sampling areas (A–F) within Knysna Estuary and within all three estuaries (Knysna, Swartvlei and Keurbooms)

Area/estuary	Total no. of seahorses	No. of males (%)	No. of females (%)	No. of juveniles (%)
A	5	0 (0)	4 (80)	1 (20)
B	55	22 (40)	21 (39)	12 (21)
C	95	44 (45)	47 (51)	4 (5)
D	46	19 (41)	21 (46)	6 (13)
E	50	23 (45)	21 (43)	6 (12)
F	29	13 (47)	14 (47)	2 (6)
Knysna combined	280	121 (43)	128 (46)	31 (11)
Swartvlei (first survey)	48	19 (39)	18 (41)	11 (20)
Swartvlei (second survey)	14	0 (0)	2 (18)	12 (82)
Keurbooms (first survey)	105	45 (43)	51 (49)	9 (9)

populations (reviewed in Foster and Vincent 2004). A higher percentage of juveniles was found during the present survey than was reported by Bell *et al*. (2001) (11% and 2%, respectively), which may be due to pushnet sampling being more suitable than visual surveys for detecting small seahorses in dense aquatic vegetation.

Comparisons of the estuaries in terms of their suitability as seahorse habitats

The comparatively high density of seahorses in the Swartvlei and Keurbooms estuaries during the first surveys may suggest that these systems provide a more suitable habitat for *Hippocampus capensis* than the Knysna Estuary, possibly because of their more extensive vegetation cover. However, the importance of the two smaller estuaries as seahorse habitats should not be overestimated. The Swartvlei population is characterised by low genetic diversity (Teske *et al.* 2003) and the effect of freshwater floods may be more detrimental in the Keurbooms Estuary than in the other two systems, because its comparatively small surface area receives more runoff than does the larger Knysna Estuary. The highest mean annual runoff estimates are 1.6×10^8 m^3 for the Keurbooms Estuary (Noble and Hemens 1978) and 1.3×10^8 m^3 for the Knysna Estuary (Pitman 1981). The negative effects of freshwater floods on the population sizes of South African estuarine fishes and invertebrates are well-documented. Possible causes for decreases in population size as a result of floods include strong currents (sweeping animals and plants out into the sea) and silt depositions (resulting in the smothering of habitat and the clogging of gills), with the effects of salinity changes being comparatively less important in species that have wide salinity tolerance ranges (McNae 1957, Grindley 1974, Hanekom 1989, Whitfield and Paterson 1995). Hence, even though the Knysna seahorse is better adapted to survive freshwater floods than are fish species of marine origin, their poor swimming ability and reliance on plant holdfasts may make them vulnerable in these situations. We suspect this is the reason why no seahorses were recorded in the Keurbooms Estuary during the second survey.

It is unlikely that the lower numbers of seahorses found in the two smaller estuaries during the second surveys was the result of the negative impacts of pushnet sampling, because no seahorse mortalities were recorded and seagrass beds are dynamic habitats that regenerate quickly (Campbell and McKenzie 2004, Cardoso *et al*. 2005). For example, a *Zostera capricorni* meadow in Wanggoolba Creek, Australia, which was completely stripped of seagrass during a flood, had completely recovered within a year (Campbell and McKenzie 2004). No signs of previous disturbance were evident during the second surveys of the Swartvlei and Keurbooms estuaries, and as Knysna seahorses probably do not maintain small home ranges (Bell *et al.* 2003), the areas sampled during the first surveys are likely to have been recolonised quickly.

If the Keurbooms Estuary does not harbour a permanent seahorse population, then the comparatively high genetic diversity of its population may be the result of gene flow from the other two systems. The fact that many mitochondrial haplotypes found in the Keurbooms population were present in the Knysna, but not in the Swartvlei, populations (Teske *et al.* 2003) suggests that the Knysna Estuary may be the main source of new colonists. The population in the Knysna Estuary is characterised by greater genetic diversity than that of the Swartvlei population, and its large area is likely to limit the negative effects of floods. This suggests that the conservation of the Knysna population is of major importance for the survival of the species.

There are two possible explanations why no seahorses were found in any of the other estuaries in the region. Firstly, these are mostly characterised by low vegetation cover (Lockyear *et al*., pers. obs.) and thus provide less habitat for seahorses, and secondly, due to their greater distance from the Knysna Estuary, they are less likely to receive new colonists once their populations have become extinct.

Directions for future research and conservation recommendations

Additional surveys should be conducted to investigate the possible effect of recent anthropogenic impacts on seahorse abundance, as well as to study naturally-occurring fluctuations in seahorse populations. In the Knysna Estuary such surveys should focus primarily on the areas surrounding the development on Thesen's Island in order to establish the effects of possible sedimentation on seahorse habitat. Further information is required on the biology and ecology of the Knysna seahorse. For example, management guidelines could be refined if the movements of seahorses within the estuary were better understood. Bell *et al.* (2003) showed that 62% of tagged seahorses were resighted in the same 10m^2 study grid during a period of 10 days, indicating some spatial fidelity. However, it is not yet clear whether Knysna seahorses maintain home ranges and whether they form pair bonds, as does the Australian seahorse *Hippocampus whitei* (Vincent and Sadler 1995). Consequently, it is at present difficult to determine whether previously-disturbed habitat that has reverted to its natural state is likely to be recolonised of its own accord, or whether it would be appropriate to translocate seahorses from within the estuary to facilitate recolonisation.

The Knysna Estuary's seahorse population should be monitored every five years to determine fluctuations in population abundance. The similar estimates of mean seahorse density found in the study by Bell *et al.* (2003) and in the present study indicate that the amount of sampling performed in the previous study (82 transect surveys) may be sufficient to obtain a reasonable estimate of the number of seahorses present within the Knysna Estuary and the same amount of sampling effort would thus be appropriate for subsequent surveys. The Swartvlei and Keurbooms estuaries are smaller and comparatively easier to sample. These estuaries could be monitored annually, to assist in determining the cause of the observed fluctuations in population sizes, so that management guidelines can be established. Particularly in the case of the Keurbooms Estuary, such surveys are required to determine whether this estuary has a permanent seahorse population or merely provides a temporary habitat when conditions are favourable. Freshwater floods may have a negative impact on seahorses, but further research is required to determine if there is a link between floods and the abundance of seahorses in this estuary.

Recreational usage of all three estuaries inhabited by *Hippocampus capensis* is significant, particularly during the peak holiday seasons. The cumulative impact of boats may significantly affect the seagrass habitats of the Knysna seahorse. Appropriate by-laws are therefore required to manage and control the environmental impacts of recreational usage of the estuaries.

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