THE ONTOGENETIC ECOLOGY AND CONSERVATION OF EXPLOITED TROPICAL SEAHORSES

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Inscription

"I am always surprised at people's surprise when they discover that the sunless depths of the great undersea trenches are not are not after all barren wastelands. It is evidence on their part not only of a lack of imagination, but of a profound sensory chauvinism, a certainty that what would be a blind and crushing void for humans must also be for other creatures.... The cure for this is to slip into black tropical waters at night and head on down. Through eye and ear pour exclamations; but as evidence of the world down there they are only as the faint scratches in a radio astronomer's headphones are to an invisible galaxy of suns.

It is a magnificently alien world..."

James Hamilton Patterson, Playing With Water,1987

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PREFACE

Thesis Format and Style

As an alternative to the traditional thesis format, the dissertation can consist of a collection of papers of which the student is an author or co-author. These papers must have a cohesive, unitary character making them a report of a single program of research. In accordance with Faculty regulations, the following text has been included in the thesis to inform the external examiners of the regulations.

1. Candidates have the option of including, as part of the thesis, the text of one or more papers submitted, or to be submitted, for publication, or the clearly duplicated text (not the reprints) of one or more published papers. These texts must conform to the "Guidelines for Thesis Preparation" with respect to font size, line spacing and margin sizes and must be bound together as an integral part of the thesis. (Reprints of published papers can be included in the appendices at the end of the thesis).
2. The thesis must be more than a collection of manuscripts. All components must be integrated into a cohesive unit with a logical progression from one chapter to the next. In order to ensure that the thesis has continuity, connecting texts that provide logical bridges preceding and following each manuscript are mandatory.
3. The thesis must conform to all other requirements of the "Guidelines for Thesis Preparation" in addition to the manuscripts.

I have chosen to submit a manuscript-based thesis which consists of five papers:

- The ontogenetic behaviour of tropical seahorses (*Hippocampus comes* Cantor, 1850) beginning their pelagic phase.
- Planktonic dispersal of tropical seahorses (*Hippocampus spinosissimus* and *Hippocampus comes*).
- The ontogeny of habitat associations in the tropical tiger tail seahorse, *Hippocampus comes,* Cantor 1850.

- Life history reference points for management of an exploited tropical seahorse.
- Modelling temporal closures and size-based harvesting options to address overfishing in an artisanal seahorse fishery

Thesis chapters were formatted using McGill University thesis preparation guidelines (http://www.mcgill.ca/gps/current/programs/thesis/guidelines/), and follow most referencing and style guidelines (e.g. not italicizing Latin expressions, Fig x. etc.) for the journal Conservation Biology. Three specific exceptions to guidelines for Conservation Biology include; capitalizing Chapter sections and the titles of books, as well as including full explanations of table elements within table captions. Conservation Biology guidelines can be found at: http://conbio.net/publications/consbio/instructions/Style.cfm

The manuscript-based nature of this thesis means that there are inevitable redundancies in referencing and acknowledgements. I have placed relevant, individually numbered appendices following chapters.

CONTRIBUTIONS OF COAUTHORS

The main ideas, analysis, synthesis (and faults) in my doctoral thesis are mine, though I have received ongoing encouragement and advice from my main academic supervisor, Dr. Amanda Vincent. I conceived and executed the five studies described in Chapters 1-5, wrote the text that precedes, intervenes and terminates these sections, executed all statistical tests and generated the figures and tables in this thesis. Dr. Vincent has provided intellectual and editorial feedback on all sections of the thesis. Chapters 1, 2, 4 will be co-authored Morgan & Vincent manuscripts, and Chapter 3 has already been published.

Morgan, S. K., and A. C. J. Vincent. 2007. The ontogeny of habitat associations in the tropical tiger tail seahorse *Hippocampus comes* Cantor, 1850. Journal of Fish Biology **71**:701-724.

The paper from Chapter 5 will be co-authored with Dr. W. Satterthwaite and Dr. D. Doak. I conceived of its research objectives, provided demographic input parameters, designed simulation scenarios and wrote all text. The original computer program needed to generate reliable growth transitions for the base projection matrix was a collaborative effort with Dr. Doak, with shared conception, and coding executed by Dr. Doak. Programs examining harvest scenarios and vital rate sensitivities were written by Dr. Satterthwaite, based on my specifications. I understood the operation of all programs and contributed minor coding input. Dr. Satterthwaite and Dr. Doak will assist with editorial revisions to Chapter 5 for publication.

Here I describe contributions to thesis logistics and data collection. In the Philippines, operational help was provided by colleagues at the Project Seahorse Foundation for Marine Conservation (PSF), who first identified Cataban Island as a potential research site, shared equipment, provided office space and cultural advice. I worked with Joel Eridiano from PSF to establish a field base and to build an initial memorandum of understanding (MOU) for research with the local village council. Thereafter, I acquired appropriate Filipino municipal research permits and undertook multiple public meetings with the help of my research assistants, Dioli Ann O. Payo and Hazel Panes. The latter aimed to level collaborative expectations with the communities of Cataban and Sagasa and to update residents about my research findings. Activities from 2001-2003 included many hours of diving, data collection and data formatting that I led, but that were also executed through the efforts of my many research assistants, volunteers and local assistants. Following fieldwork, I checked and formatted raw data, then designed databases to house this information for analyses. Supervised data entry was undertaken by three Workstudy students at UBC. I applied for, and received, animal ethics clearance from McGill University's ethics office for all field research (Appendix I).

ORIGINAL CONTRIBUTIONS TO KNOWLEDGE

This thesis represents the first in situ analysis of the early life history of seahorses, and provides novel information about the ecology of exploited tropical seahorses (*Hippocampus comes* and *Hippocampus spinosissimus*), much of it needed for conservation. Research here broadens our general understanding of the ecology, behaviour and demography of teleost fishes, using the unusual morphology of seahorses to test predictions around life history structure and strategies typically associated with tropical fishes. The conservation options that I examine for *H. comes* are relevant for other data-poor taxa exploited in multi-species artisanal reef fisheries.

Specific contributions made by this thesis include:

1. The first in situ study of the ontogenetic behaviour of a coral reef fish, during the first days of the pelagic phase.
2. Novel evidence, documented in two other marine fish family (Pomacentridae, Haemulidae), that seahorse young exhibit responses to solar cues early in their planktonic phase.
3. The first record of planktonic dispersal in tropical seahorses, with rare estimates of the density and distribution of two species in open water.
4. The first documentation of the direction and magnitude of current flows in the northern portion of the Danajon Bank, Philippines.
5. The first estimates of potential dispersal distances for two species of tropical seahorses, and comparison of these distances relative to other comparable marine fishes.
6. The first documentation of the habitat used by wild, juvenile seahorses.
7. The first surveys showing size at recruitment for tropical seahorses.
8. The first comprehensive analysis of the ontogeny of habitat by tropical seahorses use at multiple scales, with relevance to spatial management

9. Novel estimates of biological reference points needed for management of commercially exploited tropical seahorse species, including Von Bertalanffy growth parameters, length at maturity, length at reproduction, size-based reproduction, natural mortality and fishing mortality.
10. The first estimates of growth and survival rates for *H. comes* from in situ mark-recapture intervals cf previous ex situ growth information (Job et al. 2006), and length-based analysis (Meeuwig 2001).
11. A novel technical contribution in the form of a computer program (using Matlab language) that calculates growth transition probabilities for viability analysis of continuous-spawning fishes with variable asymptotic growth. Growth parameters are inferred from theory by Wang (1995). This program can be used in data-limited situations when few growth intervals are available per fish.
12. First use of mathematical modeling to explore fisheries management options for a tropical seahorse. This work is relevant to conservation for this principally tropical genus, recently listed on CITES Appendix II.
13. A demonstration of the biological value of slot sizes in seahorse fisheries: recognizing the need for further socioeconomic analysis, to evaluate its management viability
14. The first recommendations based on quantitative elasticity analyses of vital rates, prioritizing future collection of demographic data for *H. comes* and other comparable tropical seahorses.

In addition to content from these chapters, I made four other novel contributions to the scientific literature as a direct result of my thesis research. Two brief communications have been published in Environmental Biology of Fishes, documenting the current conservation status of *H. comes* and *H. spinosissimus.* Novel information used in these summaries was gathered during field research for this thesis, or collated from previously unpublished research. In collaboration with my field assistant, ongoing research started during my final field season showed sequential depletions of sea cucumbers and seahorses in a mixed-stock compressor fishery. This information has been presented orally and will be prepared for future submission to a scientific journal. Finally, collegiate ties and formative experiences at Project Seahorse also inspired an editorial piece about the role of community-engaged scholarship in Ecology.

Morgan, S. K., and Curtis, J. M. R.. *In press*. Axes of excellence: A role for students as community-engaged scholars. Frontiers in Ecology and the Environment.

Morgan, S. K., and Panes, H. M. 2007. Threatened fishes of the world: *Hippocampus spinosissimus* Weber 1913 (Syngnathidae). Environmental Biology of Fishes. DOI: 10.1007/s10641-007-9250-5. (printed online April 27 2007)

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Wang, Y.-G., M. R. Thomas, and I. F. Somers. 1995. A maximum likelihood approach for estimating growth from tag-recapture data. Canadian Journal of Fisheries and Aquatic Sciences **52**:252-259.

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It is with great pleasure that I thank my supervisor, Dr. Amanda Vincent, who has taught me much about vision, the ways of science, writing and the complexity of running a conservation organization. Your worldview has shaped me hugely and through our relationship, I have grown immensely. I have seldom seen such capacity and true dedication to not only undertaking, but achieving, conservation. Thank you for the support to strategize a degree trajectory rich with opportunities, for your contributions to this thesis and your encouragement. I look forward to a future of collaboration and wish you happiness.

I have been privileged to work during my doctorate with a supportive and insightful supervisory committee. Warm thanks and deep respect to my co-supervisor at McGill University Dr. Donald Kramer, whose experience, fairness and wisdom I was grateful for many times over. I feel very lucky to have had your support throughout my time as a student, and particularly in the final year of my degree. I know of few academics who fulfill their obligations to the academy, their departments and their students better than you Don.

Both Dr. Kevin McCann and Dr. Frédéric Guichard made insightful suggestions that stimulated my own thinking and helped to shape this thesis. My thanks to Fred for resurrecting and re-tabling concepts around ontogeny and conservation that are now found in the introduction of this thesis. I also thank Dr. Joe Rasmussen for insightful comments related to connectivity during and following my qualifying exam. I am grateful to my internal and external examiners, Dr. Lauren Chapman and Dr. Philip Munday, as well as my examining committee, who all gave of their time to improve this thesis.

A suite of funding agencies made generous contributions towards my work. In particular I would like to thank; the Natural Sciences and Engineering Research Council of Canada (NSERC), the PADI Foundation, the People's Trust for Endangered Species, the Roger Williams Park Zoo, the John G. Shedd Aquarium, and Guylian Chocolates. I was also fortunate to have been awarded funding for travel by the Department of Biology Training committee and the McGill University Alma Mater Fund. My supervisor and other grant-writing members of Project Seahorse also donated their time to create the pool of funding that allowed me to further my professional development at the Larval Fish Conference (2003), the World Fisheries Congress (2004), the International Coral Reef Symposium (2004) and the University of California, Santa Cruz (2007).

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Thank you, everyone. Merci à tous. Danghang salamat sa tanan.

ABSTRACT

This research investigated the life history and demographics of exploited, tropical seahorses. My thesis was designed to use the unusual morphology of seahorses (*Hippocampus comes* and *H. spinosissimus* in the central Philippines), to test the life history structure and strategies of tropical reef fishes. I then made direct use of ecological findings in order to evaluate risk associated with the capture of tropical seahorses for active and growing international markets.

Hippocampus comes has a broadly bipartite life history comprising three biologically distinct phases; planktonic newborns, settled juveniles and adults. Most vital rates that govern the population turnover of *H. comes* confer low susceptibility to risk. Simultaneously, aspects of abundance (range and distribution), developed parental care, behaviour and susceptibility to fishing, increase the species' inherent vulnerability.

Stage-structured matrix models examined the outcomes of temporal closures and size-based harvesting for managing artisanal seahorse fisheries. Simulations showed that when fishing occurred throughout the year at relevant intensities, slot sizes provided better protection for populations than minimum size limits, as well as greater cumulative catches over 10 year time horizons.

The ontogenetic ecology of tropical seahorses is comparable to most warm-water reef fishes, sharing: 1) a broadly bipartite life history, 2) dispersal likely to confer demographic connectivity at the scale of 10s-100s of km, 3) young that advect passively early in the pelagic phase, and 4) ontogenetic habitat associations that segregate benthic individuals into multiple ecologically distinct stages. Unusually, seahorses have: 1) a pelagic phase inferred to last between 5-10 days, among the shortest noted in reef fishes, 2) the apparent ability to orient to solar cues and 3) juveniles that associate with macroalgal beds, seldom reported as nursery grounds in tropical reef ecosystems.

For research and conservation, long-term trends in annual population abundance should be used to estimate population growth rates (λ) and to assess whether cyclic dynamics exist in seahorse populations. Approaches in this thesis are relevant to the management of data-depauperate small-scale fisheries.

RÉSUMÉ

Cette recherche a examiné le cycle biologique et l'ontogénie des hippocampes tropicaux exploités. Ma thèse visa à utiliser la morphologie particulière des hippocampes (*Hippocampus comes* et *H. spinosissimus* de la région centre des Philippines) afin d'évaluer la structure et les stratégies particulières du cycle biologique de poissons tropicaux. J'ai par la suite employé les résultats avec pertinence écologique, afin d'évaluer le risque associé avec l'exploitation des espèces d'hippocampes tropicales, destiné à subvenir à une demande internationale de plus en plus importante.

Hippocampus comes est caractérisé par un cycle biologique généralement bi-phasique, composé de trois phases distinctes: des nouveaux-nés planctoniques, des juvéniles ainsi qu'adultes benthiques. En raison des caractéristiques démographiques contrôlant les populations de *H. comes*, celles-ci ne sont probablement pas très susceptibles aux effets de l'exploitation. Par contre, certains aspects touchant à leur abondance (distribution et gamme), la présence de soins parentaux, leur comportement et susceptibilité à la pêche, augmentent la vulnérabilité inhérente de cette espèce.

Afin d'explorer diverses options de gestion pour la pêcherie artisanale ciblant l'hippocampe, nous avons développé des modèles matriciels incluant des scénarios de fermetures temporelles et de stratégie d'exploitation basée sur la taille. En supposant des pêcheries actives toute l'année, les simulations suggèrent que l'utilisation d'une fourchette de taille, plutôt qu'une taille minimale légale, assure une meilleure protection des populations et garantit le meilleur rendement cumulatif sur une période de 10 ans.

L'ontogénie écologique des hippocampes tropicaux est comparable à celle de la plupart des espèces de poissons des récifs tropicaux : (i) un cycle biologique bi-phasique/bipartite; (ii) une dispersion larvaire garantissant une connectivité démographique à l'échelle de dizaine voire centaine de kilomètres; (iii) des jeunes qui se laissent porter passivement durant leur phase pelagique; et (iv) des associations avec des habitats dépendamment des phases ontogénétiques divisant

les individus benthiques en un nombre de classes écologiques distinctes. Les hippocampes se distinguent de part leur (i) phase pélagique durant de 5 à 10 jours; (ii) la capacité de s'orienter en fonction de la position du soleil et (iii) des jeunes qui s'associent avec des bancs d'algues macro-benthiques, rarement considérés comme aire de nursery dans les systèmes récifaux tropicaux.

En terme de recherche et de conservation, un suivi à long terme de l'abondance des populations devrait être utilisé afin d'estimer des taux de croissance démographique (λ) et d'évaluer si les populations d'hippocampes suivent des dynamiques cycliques. L'approche utilisée et intégrale à cette thèse peut être utilisée afin d'améliorer la gestion et la conservation des pêcheries artisanales pour lesquelles il y a peu de données disponibles.

GENERAL INTRODUCTION

Complex Life Histories and the Conservation of Marine Fishes

Most animal species possess complex, multi-stage life histories, where development is punctuated by a sequence of distinct developmental transitions. Indeed, the most complete description of an organism lies in its life cycle, where the genome unfolds and interacts with a dynamic environment through ontogeny, across a series of life phases (Werner 1988). Shifts among these stages may be classical metamorphoses – a fundamental change in body plan or physiology – or a more general form of metamorphosis, such as rapid or gradual changes in behaviour or habitat use, that result in the distinct ecological segregation of life stages (Werner & Gilliam 1984). Complex life histories are present in taxa as different as marine fishes, terrestrial insects, and parasites: an estimated 80% of animals undergo at least one metamorphosis during their life cycle (Werner 1988). In some taxa (e.g. mammals and birds), size changes greatly with development, but the basic body plan remains largely constant. In other taxa such as fishes, arthropods and amphibians, stages can be so different that one organism functions as if it were a series of species throughout its lifetime (May 1988).

Demersal organisms in marine systems generally have complex life cycles that are broadly bipartite; they begin with a dispersive, pelagic phase and then undergo a transition which may include physical metamorphosis, into a sedentary, benthic, adult phase. This life history is present in 95% of reef fish families (Leis 1991), and is conserved across phylogenetically divergent marine taxa including cnidarians (Lewis 2006), crustaceans (Glenner & Hebsgaard 2006), echinoderms (McEdward & Miner 2001) and molluscs (Emlet & Sadro 2006). It has however, also been argued that most marine fishes actually possess a tripartite, rather than a bipartite life history, where the larval planktonic and sedentary adult phases have between them a distinct, intermediate juvenile phase. In coral reef fishes, the sub-adult stage of many species uses inshore, shallow environments such as mangroves, seagrass meadows and algal beds (Nagelkerken et al. 2000). In reality, even a tripartite life history represents a generalization, because many marine fishes progress through multiple ontogenetic phases prior to adulthood. For example, the bluestriped grunt (*Haemulon scarius*), migrates from seagrass, to mangrove prop roots, to patch reefs, in stages, before reaching adult fore-reef habitat (Mumby et al. 2004).

The stages that make up the complex life cycles of marine fishes structure demography and dynamics, at the scale of populations. As fishes grow, the distinct morphology, physiology and behavioural capacity of particular life stages govern their resource requirements. Small planktonic young optimize fitness by using their environments in very different ways from large benthic adults. This in turn determines the distribution of individuals and their vital rates across stages which govern population structure. Since it takes time for individuals to grow and move through the stages of a life cycle, structured populations effectively retain a memory of past events that interact with drivers such as conspecifics, other species, or environmental cues to generate population dynamics. Despite the complexity of life histories, most discussions about species conservation focus on distinct events, transitions or individual phases of the life history (e.g. settlement, maturity or spawning adults) (St. Mary et al. 2000). For many marine organisms we know only the most easily studied life stages.

Accounting for ontogeny and stage structure in natural populations is important because it improves both our conceptual understanding of organisms, and our capacity to manage their use. Specifically, incorporating considerations of population structure allows us to ask more realistic questions about how portions of populations respond to change or disturbance, and how proximate mechanisms govern population trends, than we could in the absence of stage-based information (Caswell et al. 1997). Ideally, conservation efforts should be targeted at critical stages, ages or events in life histories. Exercising effort at these points can have disproportionately large effects on the trajectory of populations.

Exploring these biological considerations with respect to social factors such as the economics of markets and the incentives systems that drive extraction, may generate real conservation solutions. Conversely, targeting effort at other life stages may do little to advance conservation objectives (Morris & Doak 2002). These issues are central to applied biology and management, where we are interested not only in the differences among life stages or ages of organisms, but also where to focus finite efforts to effect the most useful action for population harvest or persistence (Burgman et al. 1993).

Challenges to Understanding Complex Marine Life Histories

Improved understanding of complex marine life histories has been hampered by logistic challenges. In marine systems, comprehensive study of organismal life cycles has lagged behind similar research in terrestrial systems. The problem arises in part from the challenge of sampling the oceans. The extent, accessibility and additional dimension (depth) of aquatic environments increases the potential volume of occurrence for many species. Sampling may need to be extensive in order to gain even a basic understanding of particular life stages (e.g. Chapter 1). For example, in the planktonic phase, distributions are usually sparse, because larval young are subject to high initial mortality, and surviving propagules are then widely diffused through large volumes of water. Often only accessible life stages are studied so that aspects of the ontogenetic ecology of marine species such as larval behaviour are just beginning to receive research attention (reviewed in Chapter 2). Similarly, life stages that are difficult to locate, mark or follow, such as newly settled benthic young, present meaningful research challenges (reviewed in Chapter 3).

Using Stage Structure and Life History Information for Management

A poor factual understanding of the ontogenetic ecology of fishes and particularly of processes that regulate juvenile survivorship (Sadovy 2001), have hampered our ability to effectively manage fisheries. Historically, society has perceived the oceans as inexhaustible sources of sustenance (Lubchenco et al. 2003), and this perception has been slow to change (Harris 1999). Within science, efforts in fisheries biology have focused on stock-recruitment relationships in order to optimize profits/ biomass extracted, often under the assumption that highly fecund marine fishes reliably exhibited negative density dependent dynamics. This should mean that at low densities, fish populations rebound by producing a compensatory number of young. Despite this central tenet in fisheries, predicting year class strength remains one of the greatest challenges in fisheries (Kendall & Duker 1998). Moreover, careful studies have now refuted the notion that most marine fish families are better able to rebound from depletions than terrestrial taxa (Hutchings 2000). Little has been done in the intervening years to understand or protect non-adult life stages or their inshore benthic habitats (Diaz et al. 2003).

There can be serious consequence when extraction proceeds without properly accounting for stage structure (ontogenetic size, sex) or life history differences. These oversights have historically decreased the value of stocks or caused outright fisheries collapses. For example, when fishing skews population structure away from a balanced age/size distribution and towards juvenile classes, this tends to decrease stock stability (Aubone 2004). Over the long-term, fishing mortality on large size classes also acts as a selective pressure, inducing earlier maturation. These effects have been seen in many commercial fisheries (de Roos et al. 2006; Law 2000). Selective fishing only on male or female stages can also damage the productivity of populations. Fisheries for crustaceans are often harvested in a sex-selective manner, so that overfishing alters mating dynamics and decreases overall reproduction (Hines et al. 2003; Motz Carver et al. 2005).

Accounting for population structure is also important because fluctuations caused by cohort resonance (low frequency variation in the abundance of stage-structured populations, caused by stochastic environmental forcing), cannibalism

(Hastings & Costantino 1991), or other non-linear interactions between life stages (Gurney & Nisbet 1980; Nisbet & Onyiah 1994) have the potential to mimic or mask fluctuations in abundances caused by overexploitation or other factors (Bjornstad et al. 2004). Discounting the effects of life history information can also seriously alter our capacity to predict how populations are likely to respond to natural or anthropogenic forcing. Research now conclusively shows that recruitment predictions cannot be based solely on spawning stock biomass. Rather, life history traits such as egg quality and female condition in combination with information on population structure are required to predict stock reproductive potential (Beth et al. 2006).

Ontogenetic information is particularly informative when used a priori to target conservation action or to refine management. The key to this approach is to identify the life stages or vital rates that most influence population growth, and are therefore most likely to affect population persistence (Levin & Stunz 2005). If stage-based information can be formulated as matrix projection models, sensitivity and elasticity analyses are effective methods for understanding the relative effects of particular demographic rates on population growth (Morris & Doak 2002). A clear example of this approach was used in the late 1980's when elasticity analysis of loggerhead sea turtles (*Caretta caretta*) showed that among various life stages, oceanic juveniles exerted the greatest relative influence on population growth. From this finding came the recommendation to reduce sub-adult mortality in shrimp trawl nets over providing protection for hatchlings on nesting beaches (Crouse et al. 1987). Similar approaches are presently being used for fishes to identify critical habitat and life stages for conservation (Mangel et al. 2006).

Advances in the Use of Ontogenetic Information in Marine Systems

Novel technical, behavioural and modeling approaches have been used in the last decade that have furthered our understanding of reef fishes during the most poorly understood, sub-adult phase of their ontogeny. In particular, substantial research efforts have been made to improve our understanding of the smallest young that disperse planktonically. As well as for fundamental understanding, this interest has been driven by new acceptance of marine protected areas in developed countries and by a desire to develop effective reserve networks that achieve conservation and management objectives for beleaguered fisheries.

Methodological improvements in tagging have made it possible to mark larval fish on natal reefs and recapture them following dispersal. This has allowed the first in situ estimates of self-recruitment in marine populations. At least three types of fluorescent chemical markers have been used successfully to leave marks on otoliths and calcified structures (Adkins 1965; Hettler 1984; Wilson et al. 1987). Marking usually proceeds through direct immersion of eggs or juveniles in chemical baths (Jones et al. 1999), requiring that these life stages can be handled in the field or manipulated under laboratory conditions (Thorrold et al. 2006). More recently, enriched stable isotopes (e.g. ^{137}Ba), injected into brooding adults, have been used to create intergenerational marks in the otoliths of developing young that are retained indefinitely. Once injected, parents deliver marks to broods over a period of months and different marks can be made using different combinations of isotopes (Thorrold et al. 2006). Methods that use natural chemical signatures from ocean water, detected via laser ablation and mass spectrometry, have also yielded useful information about return rates of larvae to home reefs (Swearer et al. 1999; Swearer et al. 2002).

In and ex situ research has newly confirmed that larval reef fishes have previously unrecognized behavioural capacity. Planktonic young are now known to have substantial capacity to modify their orientation relative to land (Leis & Carson-Ewart 2003). They can be strong swimmers (Fisher et al. 2000; Stobutzki & Bellwood 1997), that are able to move effectively against ambient currents late in the pelagic phase (Fisher 2005). Very young fish also have sensory abilities that may help to modify their dispersal trajectories, assisting them to find suitable settlement sites. Olfactory cues (Gerlach et al. 2007) and the sound of reefs in particular (Simpson et al. 2005; Tolimieri et al. 2000) are among the most feasible mechanisms that larval and juvenile fishes may use to locate suitable settlement sites.

Recent research has also shown that reef fish populations, once thought to be open populations receiving recruits primarily from spawning of neighbouring or distant adults (sensu Mora & Sale 2002), have higher rates of self-recrtuiment than previously thought. Different studies have shown variously; that one third of individuals return to within two hectares of their release point (Jones et al. 2005), that invertebrate populations self-recruit on the order of 20-30 km (Becker et al. 2007), that Mediteranean reef fishes populations self-recruit 66% of their young and that 15-60% of coral reef fish return to home reefs (Almany et al. 2007; Jones et al. 1999). These studies indicate that organisms with bipartite life histories do retain some proportion of young close to parent populations, but many more studies will be needed to draw broad generalities about retention vs. dispersal of ocean fishes.

Interdisciplinary biophysical models, using oceanographic and organismal data are now being used to explore how the smallest and least understood phase of reef fish life histories structure populations. Ocean circulation models, made possible by autonomous sampling units and satellite capacity (Dickey & Bidigare 2005) are being used in at least two major reef systems -the Caribbean Basin and Australian Great Barrier Reef- to generate connectivity matrices based on the release of virtual propagules (Cowen et al. 2006; Thorrold 2006). This work is in its infancy and has only been tested empirically using genetic signatures from corals (Galindo et al. 2006). The next step will be to use direct marking to validate the predictive abilities of demographically relevant dispersal models (Almany et al. 2007).

Theoretically, spatial marine planning should also incorporate multi-specific life stage information. Optimization methods have been developed that combine information about species' ecology with stakeholder objectives to prioritize options (e.g. MARXAN, , Ecopath with Ecosim and Ecospace (EwE)). These approaches have the capacity to incorporate ontogeny, but in practice, rarely do so.

Reef Fisheries, Seahorses and Conservation

Our substantial ecological ignorance of many reef species, combined with dynamic and increasing extractive pressure, presently challenge research, management and institutional support of fisheries. Information on the ontogenetic ecology and connectivity of coral reef fishes is most available in regions with substantial resources, while the greatest human dependence on coral reef fishes is in developing countries. Here, little is known about the basic life history or demography of many taxa captured in tropical, multi-species, small-scale fisheries. These artisanal fisheries provide essential protein and livelihoods for approximately 120 million people (FAO 1996). It is currently estimated that 64 % of coral reef fishes are overexploited, with pressure expected to increase by 160 % in island reef fisheries by 2050 (Newton et al. 2007)..

Capacity to manage reef fisheries is further challenged in species with life history traits that increase vulnerability to exploitation. Species with high vulnerability decline in abundance faster than others, under comparable fishing pressure (Cheung et al. 2005). Traits normally associated with vulnerability to exploitation include large body size, greater longevity, greater age at maturity and slower growth rates (Jennings et al. 1999; Reynolds et al. 2005). However, particular life stages, behaviour or reproductive modes may also increase vulnerability to fishing. For example, fishes in the families Serranidae, Lutjanidae and Lethrinidae exhibit a spawning aggregation phase. This portion of the life history makes it possible for fishers to remove 20-30% of aggregations over only a few days (Sadovy & Domeier 2005). Similarly, fishes that change sex with size, which are prevalent in tropical regions, may be threatened by size-selective fishing. If the largest individuals of a given sex are removed from populations, this can create sperm or egg limitation in the population, decreasing reproductive output (Alonzo & Mangel 2004; Molloy et al. 2007; Vincent & Sadovy 1998).

Current Knowledge of the Stage-Based Ecology of Tropical Seahorses

Seahorses are one example of the many cryptobenthic fishes captured in small-scale, multi-species artisanal fisheries, about whose ontogenetic ecology we know relatively little. In the literature, there is debate about the basic structure of the seahorse life history. There is recent evidence of seahorse young in the plankton (Kanou & Kohno 2001; Perez-Ruzafa et al. 2004; Vandendriessche et al. 2005), although this need not mean that the majority of young move planktonically. More limited research indicates that seahorses do not have a planktonic phase and settle immediately after release from fathers (Golani & Fine 2002; Russell 1976). If indeed seahorses do possess a pelagic phase, we have no understanding of the temporal or spatial scales of dispersal or how behaviour may inhibit or promote movement. This information is vital for understanding the demographic and genetic connectivity of populations, and to inform spatial management.

Our present knowledge of settled juvenile seahorses, is largely limited to patterns of allometry, growth and husbandry, studied ex situ in aquaculture facilities (Choo & Liew 2006; Woods 2003a, b; Woods 2000b) (Table 1). In situ, there may be an intermediate phase of the life history when juvenile seahorses settle from the water column to the benthos, and use habitat distinct from that of adults. The existence of distinct juvenile habitat has been inferred from the relative dearth of small animals among adults (reviewed in Chapter 3), and because most juvenile reef fishes exhibit ontogenetic shifts through various nearshore environments prior to adult residency on reefs (Adams et al. 2006; Dahlgren & Marr 2004; Kaufman et al. 1992). Temporal aspects of the juvenile ecology of seahorses, such as recruitment dynamics, also remain poorly understood. Preliminary evidence from landings data indicate that tropical seahorses may display at least one annual recruitment pulse (Project Seahorse, unpublished data). How the timing of this settlement period interacts with aspects of habitat use and fisher behaviour requires further study.

The adult portion of the seahorse life cycle is better understood than the juvenile phase (Table 1) and has been studied from a variety of perspectives, mainly in temperate systems. Research has addressed the biology, structure, reproduction, fishing and trade of mature animals (Bell et al. 2003; Curtis & Vincent 2005; Curtis & Vincent 2006; Martin-Smith & Vincent 2005; Moreau & Vincent 2004; Perante et al. 2002; Vincent et al. 2005). Vital rates are available for few species although demographically, most types of seahorses remain unstudied (but see Curtis & Vincent 2006). The apparent sex role reversal of seahorses has also promoted extensive observation of adult reproductive behaviour, both in and ex situ (Vincent et al. 1992; Vincent 1990, 1994b; Vincent & Sadler 1995; Wilson et al. 2003). Limited work has investigated the incidental and directed catch of seahorses in one fishery (Baum et al. 2003a), although some seahorse exploitation has been well characterised (Meeuwig et al. 2003; Vincent et al. 2007) and the international trade of (mainly large) dried seahorses has been subject to ongoing research over the last decade (Baum & Vincent 2005; Giles et al. 2005; McPherson & Vincent 2004; Vincent 1996).

There is a real need to understand seahorse life histories because many species face conservation concerns arising from overfishing and habitat loss. The majority of species in the genus *Hippocampus* are traded. In the mid-1990s, it was estimated that approximately 20 million animals were moved through markets every year, with ca. 90% of animals sold dried as traditional medicine. The remaining 10% was sold alive as aquarium pets or as dried curiosities (Vincent 1996). It is challenging to infer the global impact of this trade on wild populations because we have little information on in situ densities. Regional declines are known to have been associated with the onset of fishing (A. Maypa, unpublished data, Giles et al. 2004). These trends have been recognized by the formal listing of all seahorses on the IUCN Red List of Threatened Species, with all but one species categorized as either Vulnerable or Data Deficient (Lourie et al. 2004). In a precautionary response to the substantial volume of animals in trade, and the likelihood that exploitation is presently the main threat to the genus, all seahorses (*Hippocampus* spp.) were listed on Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) in November of 2002.

Tropical seahorses particularly, face greater threats from exploitation than temperate species because they can be fished profitably even at low densities in developing countries and are seldom protected via robust legislation or enforcement. Perhaps not coincidentally, all fourteen of the species recently seen in surveys of the dried trade (Morgan & Vincent 2006) exhibit either partially or fully tropical distributions and are captured principally in developing regions.

The shallow-dwelling tropical tiger tail seahorse, *Hippocampus comes* Cantor, 1850, and its deeper-water congener, *Hippocampus spinosissimus* Weber 1913, are both heavily traded. *Hippocampus comes* is the principal species sold from the Philippines, which in the last major review of trade, was the second largest exporting country globally (Vincent 1996). *Hippocampus comes* is well studied compared with other warm-water seahorses and research in the central Philippines has documented multiple population declines of 65-100% over periods of approximately 20 years, following the onset of fishing (A. Maypa, unpublished data). *Hippocampus spinosissimus* has received little research attention (but see Do et al. 2006; Morgan & Panes 2007), but given its geographically broad, deeper-water distribution, it may face substantial threats from trawl bycatch, a major source of dried seahorses in Southeast Asia. Other tropical seahorse species, including *H. trimaculatus, H. histrix, H. kelloggi* and *H. kuda* are likely to face comparable threats from fishing and bycatch.

Limited demographic understanding of the life history of tropical seahorses has restricted our ability to effectively assess and manage these exploited fishes. Some of the vital rates of seahorses indicate resilience (e.g. rapid growth, early maturity, short generation time, small size Curtis & Vincent 2006), while others such as reliance on benthic holdfasts, specialised and lengthy parental care and mate-pairing with its attendant widowing effects if one partner is fished, could increase susceptibility to over-exploitation (Foster & Vincent 2004b). Thus far, management has been proposed based on common sense and rules of thumb (Foster & Vincent 2005), but not by quantitatively exploring the interactions between population biology, stage-based needs and policy alternatives (but see Curtis 2004).

Thesis Structure and Objectives

Here, I have examined how quantification of ontogenetic ecology can improve our understanding of reef fish ecology and our ability to manage tropical fisheries. I used seahorses, a charismatic flagship species (Martin-Smith & Vincent 2005) with unusual upright morphology, to test the typical life history structure associated with tropical reef fishes. I also aimed to explore feasible management options for the real problems faced by tropical seahorse populations, relevant to other data-depauperate taxa exploited in multi-species artisanal reef fisheries. Specifically, my objectives were to a) characterize stages in the life cycle of tropical seahorses as well as behaviour and ecology relevant to different life stages (Chapters, 1 (planktonic juvenile behaviour), 2 (abundance and distribution of planktonic juveniles), 3 (abundance and distribution of settled juveniles and adults)) b) comprehensively quantify the stage-based demographic rates of a tropical seahorse and understand how the life history strategy of these unusual fish does or does not confer vulnerability under exploitation (Chapter 4) and c) prioritize management options for tropical seahorses, which are heavily fished in the central Philippines (Chapter 5). More broadly, I aimed to use seahorses to examine d) the ubiquity of a bipartite life history in reef fishes (Chapter 1, 2) e) how behaviour has the potential to affect reef fish dispersal early in the planktonic phase and f) the implications of stage-based habitat use in reef fishes. My work focused on the tiger tail seahorse, *Hippocampus comes* Cantor, 1850, with incidental research on a sympatric congener, the hedgehog seahorse, *H. spinosissimus* Weber 1913.

This thesis was structured around the life cycle of tropical seahorses, with effort allocated to sequential stages of the life history. In particular, my work focused on the least understood portion of the life cycle, the juvenile phase, with three out of four life stage chapters inspired by fundamental questions about juvenile ecology (Chapters 1-3). Two chapters directly investigate the adult stage (Chapters 4-5) and the final chapter (Chapter 5) uses an improved understanding of the ontogenetic ecology of *H. comes* to model the effects of present and potential management on persistence.

Many of the methods used in this research should be feasible to use when making preliminary and much needed quantitative assessments of "S" fisheries (sensu Orensanz et al., 2005): stocks that are taken in small-scale fisheries, are spatially structured and sedentary. These fisheries are sometimes considered unmanageable (Orensanz et al. 2005). Approaches used here should also be applicable to populations that are cryptic, found naturally at low densities, or that can be fished beyond commercial limits (hand-gathered to extinction).

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Table 1. Summary of life history research on seahorses from temperate and tropical zones, available in the published literature.

	Temperate juveniles	Temperate adults	Tropical juveniles	Tropical adult
Dispersal/ movement	Boisseau 1967; Kanou & Kohno 2001; Perez-Ruzafa et al. 2004; Vandendriessche et al. 2005	Curtis & Vincent 2006; Vincent et al. 2005		Perante et al. 2002
Behaviour		Vincent 1995		Tran et al. 1995
Habitat Use		Curtis & Vincent 2005 Bell et al. 2003; Martin-Smith & Vincent 2005; Moreau & Vincent 2004		Dias & Rosa 2003; Perante et al. 2002
Growth	Filleul 1996; Woods 2003b	Curtis & Vincent 2006	Choo & Liew 2006; Job et al. 2006; Job et al. 2002; Mi 1993	
Reproduction	n/a	Boisseau 1967; Curtis & Vincent 2006; Lockyear et al. 1997; Poortenaar et al. 2004; Texeira & Musick 2001	n/a	(Perez-Oconer 2002)
Survival	Curtis 2004; Woods 2003a, b; Woods 2000a	Curtis & Vincent 2006; Martin-Smith & Vincent 2005; Woods 2003c		

LINKING STATEMENT I

Recent research has shown that larval fishes, particularly species that inhabit coral reefs as adults, have substantial behavioural capacity that can modify dispersal trajectories – either to promote or inhibit travel. Since most fishes are poorly developed when they initially enter the plankton as either gametes, floating eggs or yolk-sac larvae, behaviour is believed to be most influential at the end of the pelagic phase, prior to settlement. In contrast, seahorses develop directly inside parents brood pouches and are born as well developed juveniles. Therefore, from the earliest days of their pelagic phase, behaviour may play a meaningful role in their dispersal trajectories.

I started my thesis at the beginning of the seahorse life history, seeking evidence of a planktonic phase in *Hippocampus comes* and an understanding of how behaviour, if present, may mediate pelagic movement. I also wanted to know whether and how behavioural capacity changed with age. Since the activities of larval fishes are strongly affected by experimental conditions, this research was designed to take place in the field, using wild-reared young from local fathers, to document performance and position typical of activities in reef waters. These types of data, observed in natural conditions, are likely to provide the most realistic behavioural inputs with which to model movement between networked marine populations. Findings can also be compared with analogous information from ex situ studies of behavioural development in coral reef fishes.

CHAPTER 1

THE ONTOGENETIC BEHAVIOUR OF TROPICAL SEAHORSES (*Hippocampus comes* Cantor, 1850) BEGINNING THEIR PELAGIC PHASE

ABSTRACT

Many marine organisms have a bipartite life history where small mobile individuals disperse in the plankton. The larvae of tropical fishes have substantial ability to affect their dispersal trajectories, particularly late in the planktonic phase prior to settlement. Here we investigated whether behaviour early in the pelagic phase, had the potential to affect dispersal in seahorses. Characterizing when active behaviour begins is relevant to understanding connectivity of marine populations. Using a reef fish that is unusually well developed at birth, we observed the in situ ontogeny of orientation in the tiger tail seahorse, *Hippocampus comes* Cantor, 1850. At ages ranging from 1-4 days after birth, young were released from their natal reef, and then observed for 15 minutes. We collected data on depth, orientation relative to ambient currents and the sun, swimming ability and feeding. Like most coral reef fishes larvae, seahorse young moved immediately into the water column and did not grasp structures on the benthos. We noted meaningful differences in the circular orientation of young during morning versus afternoon observations, seen previously in pomacentrids and haemulids. Sensitivity to polarized fields may be useful to shallow reef-associated species, for prey capture, courtship, spawning or orientation in complex three dimensional habitats. The absence of sustained swimming, observed bursts of critical swimming associated with prey capture and daily ontogenetic development of orientation suggest that newborn seahorses exhibit behaviours that optimize feeding, while advecting passively. Our field results corroborate ex situ research showing that early in the pelagic phase, even particularly well-developed reef fishes do not exhibit behaviours likely to affect their dispersal trajectories.

INTRODUCTION

The behaviour of individual larval fish, along with oceanographic processes, help to structure reef fish populations (Leis & McCormick 2002). Larval fish were once thought to act as passive particles, but recent research has shown their capacity to behave in ways that meaningfully affect their movement trajectories (Fisher 2005; Leis & Carson-Ewart 2003; Leis et al. 2005; Leis et al. 2007). The connectivity of fish populations has important implications for the biogeography of species, the genetic and evolutionary processes that regulate biodiversity, the spread of invasive species and the demographic supply to and from patches that sustain populations (Cowen et al. 2006). Understanding these source-sink dynamics on appropriate scales has important consequences for the management of fisheries effort and the design of marine protected areas.

Late stage planktonic young exhibit behaviours that vary with ontogeny, taxonomy and morphology (Bay et al. 2006; Fisher et al. 2005; Simpson et al. 2005). Close to settlement, larval fish behave in ways that may increase their retention, promote their dispersal, or affect mortality (Leis & McCormick 2002). For example, young can vary their depth (Leis et al. 2006; Leis et al. 1996), change their position relative to predators (Leis & Carson-Ewart 1998; Leis & Carson-Ewart 2001) and affect their distance and swimming trajectories relative to land (Leis et al. 2006). Late phase larvae are also strong swimmers. With considerable endurance, planktonic larvae have the ability to swim at speeds of more than 14 body lengths per second or 60 cm s^{-1} (Leis & Carson-Ewart 1997) for periods of up to 271 hrs (11.3 days) (Stobutzki & Bellwood 1997). At these speeds, larval fish can be “effective swimmers” - moving at rates that exceed ambient currents - conferring the potential to exert control over their locomotion (Fisher 2005). All of these abilities have important fitness implications and are likely to be strongly affected by selection during the planktonic phase of the life history.

Comparably less work has addressed the behavioural abilities of reef fishes immediately after birth. In fact, we could find only one recent study that observed the in situ behaviour of a reef fish – a pomacentrid damselfish, *Amblyglyphidodon curacao* - early in its pelagic phase, and even this used young already 11-15 days old (Leis et al. 2007). Other research has inferred the onset of active behaviour midway through the pelagic period, via differences in the vertical distribution of preflexion versus postflexion larvae (Paris & Cowen, 2004) and through ex situ observation (e.g. in Fisher 2005). Predicting the onset of active larval movement is key to accurately understanding the dispersal potential of fishes (Cowen et al. 2006). Furthermore, ontogenetic shifts in behaviour over time have been examined for a very few reef fish families, all with perciform (perch-like) morphology (Fisher et al. 2000). Most of this research has been conducted in laboratory environments (Clark et al. 2005; Fisher et al. 2000) where young may not be presented with appropriate stimuli or space to behave as they would in open ocean conditions. In the wild, only two studies have investigated the ontogenetic behaviour of larval fish, both using captive-reared young (Leis et al. 2006; Leis et al. 2005).

Our research focused on seahorses (*Hippocampus* spp.); demersal brooding fishes with advanced parental care that release large, direct developing young. Most marine demersal fishes hatch from pelagic eggs at small sizes (1 - 3 mm) and possess little initial behavioural capacity (Leis et al. 2005). In seahorses, behavioural capacity may exist immediately upon emergence from male pouches'. Contradictory accounts of behaviour exist in the literature, where some authors infer that members of this genus possess a pelagic phase (Barlow 1981), while others suggest immediate settlement (Golani & Fine 2002; Russell 1976). Regardless, seahorses are large at birth, even relative to other fishes with parental care (Foster & Vincent 2004a). They are also well-developed, having undergone metamorphosis inside the male's ventral pouch. This presents the opportunity to investigate the earliest boundaries for the onset of planktonic behaviour in reef fishes. The unusual morphology and upright swimming of seahorses also suggests that they may exhibit behaviours unique among young reef fishes. This could broaden our awareness of behavioural diversity in these taxa. Understanding dispersal-related behaviours should contribute to conservation efforts for seahorses which are commonly overexploited for international trade (Vincent 1996).

Our objective here was to obtain the first field observations relevant to dispersal, in a fish with the potential for developed behavioural capacity, early in the pelagic phase. We examined how seahorse behaviour changes with development and assessed how these changes might affect dispersal trajectories. Specifically, we examined whether there was in situ evidence in newborn *Hippocampus comes* Cantor, 1850 for: a) immediate settlement of seahorses, b) control of vertical position, c) horizontal translation (displacement from one point in space to another) and d) competency to orient in the water column relative to ambient currents and environmental cues. We measured how these behaviours varied with seahorse age. Such data (and our accompanying behavioural observations of foraging, predation and rafting) are only available for a very few reef fish species (Leis et al. 1996).

METHODS

Study Site

The research took place from 25 April-31 May 2003 at Cataban Island (10°13.75'N, 124° 23.36'E), a small coral sand atoll in the double barrier reef system of the Danajon Bank, Bohol province, in the central Philippines (Fig. 1). Cataban Island is part of the inner Calituban reef and lays ca. 5 km from the Bohol mainland. The island is surrounded by an extensive shallow water reef flat with seagrasses close to shore, macroalgal beds at the edge of the reef flat (*Sargassum* spp.) and coral heads on the reef slope (*Porites* spp., *Seriatopora* spp., *Acropora* spp.). At ca. 250 m offshore, the reef crest drops to a 5-6 m sandy/silty bottom that slopes gradually to 10-14 m (Green et al. 2000) with occasional channels to 20 m. During the study period, marine salinities ranged from 30.3-34.8 ppt, and sea temperatures ranged from 29-32° C; neither parameter exhibited vertical stratification (S.K.M., unpublished data).

Study Species

We examined the behavioural ontogeny of the tiger tail seahorse *Hippocampus comes*. This species is distributed throughout Southeast Asia and within its range, is believed to be most abundant in the central Philippines (Lourie et al. 2004). *Hippocampus comes* is listed as “Vulnerable” on the IUCN Red List (IUCN 2006), and all seahorses were recently listed on CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) Appendix II, which took effect in May 2004.

The extreme form of parental care seen in seahorses that brood young in a ventral pouch (Foster & Vincent 2004a), coupled with strong site fidelity in mature *H. comes*, makes it possible to capture pregnant males from monitored populations, and release wild young from their natal reef. Seahorse young develop directly (sensu Balon 1999) inside male brood pouches prior to release, so they are not larvae, but rather small juveniles at birth. The term *juvenile* often connotes young late in the pelagic phase about to settle or having just settled: here we use the generic expressions newborn or young to refer to study subjects that were morphologically developed, but newly released.

Field Methods

Collecting Young

We obtained most young from pregnant males in advanced stages of pregnancy that we had been monitoring individually inside a marine reserve at

Cataban Island. Experienced seahorse fishers also caught males from fishing grounds. Surveys started between midnight and 03:00, when *H. comes* in this region are most accessible and lasted 2-5 hours. To facilitate returns, GPS co-ordinates of holdfasts with males were recorded, then marked with an underwater float.

After transport in buckets, 2-4 brooding males were held underwater in cylindrical cages (35 cm diameter X 50 cm) at Cataban Sanctuary (Fig. 2). These cages were made from plastic chicken mesh, encased in a mesh bag with a drawstring opening and with sponge and loose coral fragments as holdfasts. Mesh size of the cages (2 cm) and bag (0.5 cm) was large to allow the free passage of prey items. Cages were located in 1.25-2.5 m of water, depending on the tidal cycle, in an area occupied by wild *H. comes*. Males were checked twice daily (06:00-08:00, 16:30-18:30) and moved from holding cages into a rectangular birthing box (40 cm X 30 cm X 30 cm) late in pregnancies. Newborns were then transferred by squeeze bottle to nursery cages (22 cm X 25 cm X 27 cm) and males were returned to their original holdfast on the next survey evening. Broods from a total of 9 males were divided evenly into five nursery cages. Cages were fanned daily to remove accumulated sediment on mesh. Single individuals for observation were haphazardly selected by blindly inserted squeeze bottles into nursery cages and aspirating the individual closest to the nozzle. Cages were used in rotation.

Focal Observations

We performed focal observations on the in situ behaviour of a total of 138 different young, and analysed a subset of approximately half of all these (n = 63), all from ebb tides. Individuals born anywhere between sunset (18:30) of the night prior, and dawn (05:30) of the same day that they were followed, were called Age 1s. On subsequent days, individuals were called Age 2, 3 and 4. All focal observations lasted 15 minutes, occurred between 07:45 and 19:00 and had the same start point (10°13’505 N, 124°23’030 E) that was located centrally within Cataban Island’s marine sanctuary. Young were released on an ebb tide, where currents moved in a generally west-east direction over a reef flat. Subjects were removed from holding cages and placed inside a 20 cm X 10 cm X 5 cm clear Plexiglass box that was held stationary above the release site for > 1 minute before opening. A recorder and observer, both on S.C.U.B.A., faced each other approximately 3 m apart (Leis et al. 1996). The observer released the seahorse non-directionally, 30 cm from the benthos by using a long handle to depress the hinged floor of the box, allowing the seahorse to swim down and out at will.

The observer counted the total number of feeding strikes (Bergert & Wainwright 1997) during the trial. Fixed-interval time point sampling (sensu Martin & Bateson 2001) was used by the recorder to note current direction every 2 minutes, and orientation and depth every 30 seconds. For orientation and depth, interval duration was chosen as the shortest time that practiced recorders needed to accurately obtain measures. This is typical of behavioural time-sampled studies, and provided a record that approximated continuous observation so that results could be represented as frequency distributions (Martin & Bateson 2001). Seahorse orientation was taken as the bearing indicated by the snout, while current direction was measured as the bearing of obvious waterborne particulate matter downstream, relative to the visible benthos. All measurements were recorded to the nearest 10 whole degrees, as a positive degree deviation from magnetic north: declination in this part of the Philippines in 2003 was less than one degree from true North. Depth was measured to the nearest 0.075 m. At the end of each observation, subjects were collected by squeeze bottle and preserved in 10 % seawater-buffered formalin for measurement. GPS waypoints taken at the beginning and end of each trial were used to corroborate in situ measurements of overall current speed and direction.

Measurements and Analysis

We photographed young with a scale rule using a Sony XL-77 digital camera mounted on a Leica™ MZ8 dissecting microscope. Contorted individuals were lightly pressed between two layers of plexiglass and measured using ImageJ software available at http://rsb.info.nih.gov/ij/. Standard length was measured as the combined head length (HL), trunk length (TrL), and tail length (TaL), following trunk and tail curves (Lourie 2003)

Circular and other statistics followed (Batschelet 1981) and Zar (1999), using Oriana software™ (vers. Kovach Computing Services), SPSS™ 14.0, Systat™ 11.0 and Sigmaplot™ 8.0. Sample sizes varied between analyses, because we used only comparable follows in each analysis (e.g. releases on the same tidal cycle, all feeding individuals, etc.). Some trials were also excluded when individuals became ineffectual at remaining vertical in the water column, or exhibited vertical or horizontal "tumbling" not observed in young reared successfully ex situ. Similar exclusions were made by Leis et al. (1996). To avoid autocorrelation in sequential depth measurements, we obtained a mean of all depth values for each individual, then pooled them within age class to generate an overall average depth per age, and used ANOVA to analyse the relationship between age and depth.

Evidence for upstream swimming was analysed in two ways based on orientation data. Circular chi-squared tests examined whether the distribution of seahorse bearings for a given day age differed significantly from current distributions at the beginning and end of trials. For degree classes with few bearings (<5), we also used Watson-William's F-tests to examine whether, by age, angles differed significantly between mean seahorse bearings and mean current bearings, at the start of observations and also after 15 minutes. Grouped data at intervals ≤ 10° are acceptable inputs for Watson-William's F-tests (Batschelet 1981).

The ontogeny of orientation and responses to solar cues were examined by testing differences in the angular dispersion of bearings via Wallraff tests that are a circular analogue of Mann-Whitney or Kruskal-Wallis tests for two or more samples, respectively (Zar 1999). Consecutive bearings recorded from the same individual during a focal observation may be autocorrelated. Therefore, we used autocorrelation charts (Systat 11.0™) to test for dependence among bearings for individuals. Trajectories were tested at all lags k (k = 0, 1,…., k) for k not larger than N/4, where N = the total number of observations within a series. Here, we tested lags from 1-7 for our focal observations which had n = 30 bearings. Ideally, >50 observations per series is preferable for time series analysis (Box & Jenkins 1970), but this approach has been used for comparable and shorter behavioural series for fishes (Leis 2004; Leis et al. 2007). We found that only 19 % of observations (n = 12) showed evidence of temporal autocorrelation (lags 1-4), with most series (14.1 %, n = 9) at lags ≤ 2. For all series, data were discounted at relevant intervals to remove autocorrelation structure. For example, at a lag of 1, we removed every other bearing. At a lag of 2, we analysed only every third bearing etc. (Leis 2004; Leis et al. 2007).

When our hypotheses invoked multiple comparisons (e.g. angular dispersion between pairs of multiple day ages) we used Holm-Bonferroni adjustments, which are used widely in the health sciences and avoid some of the more restrictive and contentious assumptions of Bonferonni corrections (Aickin 1999; Perneger 1998).

RESULTS

A total of 138 trials were undertaken over a period of 37 days, with young from 9 males. Individuals travelled from 18.0 to 264.5 m, moving a mean (± SE) distance of 115.2 ± 6.9 m in 15 minutes. The mean speed of follows was 0.128 ± 0.008 m sec^{-1}, ranging approximately one order of magnitude from 0.02-0.29 m sec^{-1}. No individuals tried to settle on, or shelter near, divers, and diver position varied haphazardly (as per Leis et al. 1996). Most individuals fed during trials and none exhibited body position comparable to flight-swimming by adult *H. comes* moving away from divers (S. Morgan, pers. obs.).

Age 1 individuals consistently swam with tails curled almost entirely under the body trunk, held left or right of the vertical body axis, parallel to the bottom. The animals at Age 2 unfurled their tails more often, and were able to "dive" from the surface of the water by orienting the body to a more horizontal position, with the tail almost in a straightened swimming position seen in adults. Age 2 individuals in extended body positions, rarely oriented with heads below horizontal. Age 3 and 4 individuals swam with tails mainly extended, curling the tip only to orient left or right. These age classes were observed to dive shortly after contact with the surface (descending approximately 1 m in 15 seconds) with tails extended and heads oriented past horizontal, directed towards the seafloor.

Vertical Position

Hippocampus comes were planktonic immediately upon release from the pouch. All young were positively buoyant and found on the upper inner mesh ceiling of cages, and all young rose rapidly to the surface during in situ trials, despite an opportunity to adjust to the release depth. Indeed, 98.5 % of young (n = 138) showed no attempts to settle immediately to the benthos, despite the proximity of available and suitable reef and algal habitat. The remaining two animals (Age 2 & Age 3), swam downwards and rested on the sandy bottom following release. When re-released after 15 minutes, they did the same thing, in both cases, actively thrashing their tails for short periods of 10-15 seconds.

All age groups rose rapidly to the surface in the first two minutes after release and followed similar descent trajectories over the subsequent duration of observations (Fig. 3). Mean start depths by age ranged from 1.88-2.04 m due to tidal variation, but did not differ significantly among ages (ANOVA, $F_{3,59}$ =

0.527, p = 0.665, n = 63). Age 1 young rose closest to the surface, and most rapidly at a rate of 0.88 m min^{-1}: Age 4 young rose the least and rose most slowly (0.60 m min^{-1}). After 5 minutes, trajectories stabilized relative to the first few minutes of trials, then converged to similar depths with time.

Average depth varied significantly among ages (ANOVA, $F_{3,59} = 10.74$, $p<0.0001$, n = 63), with younger individuals found closer to the surface. Age 1 young were found at the shallowest depths (X ± SE = 0.30 ± 0.06 m, n = 13) followed by Age 2 (0.63 ± 0.06 m, n = 18), Age 3 (0.78 ± 0.06 m, n = 18) and Age 4 individuals (0.80 ± 0.08 m, n = 14) (Fig. 3). Holm-bonferonni corrected Tukey tests showed differences to be significant only between Age1 individuals and all other ages. Developmental age (regression, $R^2 = 0.04$, p = 0.05, n = 83), rather than size (regression, $R^2 = 0.0004$, p = 0.84, n = 83), was a better predictor of position in the water column, although behaviour varied substantially among individuals.

Distance travelled was related to position in the water column, with deeper individuals moving farther (regression, $R^2 = 0.16$, p = 0.003, n = 55). Age 1 young appeared to travel the least (mean ± SE = 107.8 ± 17.0 m) (123 ± 12.8 m -137 ± 12.6 m), but statistically significant differences were not detected amongst different age groups (ANOVA, $F_{3,52} = 0.83$, p = 0.49, n = 56).

Horizontal Swimming

In general there was no evidence for translation through horizontal swimming. Many individuals attempted to swim upstream immediately upon release, and some were able to hold a stationary position relative to the bottom for short periods, especially older individuals. However, even the strongest swimming individuals were generally unable to maintain their position in ebb tide flows for >30 seconds, and no individuals swam forward against ambient currents. For all ages, the mean bearing between seahorse and current was significantly different immediately after release, but not at the end of trials, reflecting short bouts of upstream swimming (Table 1).

Orientation

Seahorse young showed significant ability to orient while advecting passively along the bearing of ambient currents. Older seahorses turned more, resulting in statistically significant increases in angular deviation as a function of day age (Walraff test, $H = 38.09$, $df = 3$, $p<0.001$). Total bearings showed a downstream bias for Age 1 and 2 individuals that diminished with age, resulting in bearings that were more uniformly distributed by Ages 3 and 4 (Fig. 4). The mean circular standard deviation of total bearings increased from 68.8° at Age 1 ($n = 331$), to 85.28° at Age 2 ($n = 473$), to 101.0° at Age 3 ($n = 506$) and to 103.1° on Age 4 ($n = 392$) (Fig. 4). This can also be expressed as a decrease in the length of the mean vector for each day age, r, where $r = 0$ indicates full dispersion and $r = 1$ indicates no dispersion. These r values decreased across day ages (Age 1: $r = 0.48$, Age 2: $r = 0.33$, Age 3: 0.21, Age 4: 0.19). Holm-Bonferroni corrected multiple comparisons on all bearings were significant between all but the two youngest and two oldest day ages (Age 1 vs. 2, Age 3 vs. 4) (Table 2). Neither circular standard deviation (circular-linear correlation, $r = 0.18$, $p = 0.16$, $n = 59$), nor depth (regression, $R^2 = 0.0003$, $p = 0.88$, $n = 85$) showed a meaningful relationship with the standard length of young. The speed of current during observations (and its potential effect on bearings or capacity to turn) was not significantly different among ages (KW ANOVA, $H = 3.62$, $df = 3$, $p = 0.305$).

The orientation patterns of *H. comes* young changed with the time of day (Fig. 5). In both morning and afternoon, young oriented in similar mean directions ($\mu_{am} = 81.1°$, $\mu_{pm} = 74.5°$) corresponding to a generally downstream direction. The difference was, that the angular dispersion in bearings increased significantly from the morning to the afternoon (circular standard $\text{deviation}_{\text{morning}} = 79.8°$ vs. circular standard $\text{deviation}_{\text{afternoon}} = 97.9°$) (Wallraff test, $U = 336572$, $p = 0.005$, $n = 1702$). In the afternoon, observed individuals showed a greater spread of bearings which were distributed in a largely symmetric manner around the angular mean (μ). Neither current direction (Watson-Williams F-test, $F_{1,62} = 0.025$, p = 0.88) nor age of young (Pearson $X^2_{0.05,3} = 2.24$, p = 0.53 (2 tailed)) varied significantly between morning and afternoon follows.

Behavioural Observations

Foraging

At all ages, seahorse young attempted to actively feed on unidentified prey items in the water column. When approaching food items, young undertook short burst swimming, moving < 2 body lengths, extending the head relative to the tail towards potential prey: 94 % of subjects were observed engaging in visible head snapping and striking; behaviour associated with feeding in seahorses. Exogenous feeding commenced immediately after release on day 1 (78.9 % of Age 1 individuals fed). Feeding rates for all ages exhibited negative exponential distributions, with most individuals feeding infrequently and a few individuals feeding often. The upper 20 % of feeding rates ranged from 11 (Age 4) – 21 (Age 3) bites per 15 minutes. On average, feeding rates were comparable among ages 1-3 (X ± SE = 6.04 - 6.88 ± 1.14 - 0.98 strikes per 15 minutes) and half as rapid in individuals of Age 4 (3.88 ± 0.78).

Predation

We observed four instances of predation on *H. comes* young in 138 observations, all by Pacific Gregory Damselfish, *Stegastes fasciolatus* Ogilby 1889, and all within 50 cm of the bottom. Two individuals (Age 2 and Age 4) were eaten while the others (Age 3 and Age 4) were ingested and then rejected.

Rafting

Rafting was observed on two occasions, both on 29 May 2003, a day in which surface slicks of floating debris were unusually comprised of short fragments of *Syringodium isoetifolium* (Aschers.) Dandy at the surface. Typical floating debris for the area includes mangrove leaves (*Rhizophora stylosa* Griff.) and large seagrass fragments (*Thalassia hemprichi*i (Ehrenb.) Asch. and *Enhalus acoroides* (L.f.) Royle). Both seahorses were one day old and rafted for 2.25 minutes and 30 seconds respectively. The second individual tried unsuccessfully to raft again two minutes later. Three other seahorses observed on the same day (one from the same brood) were not seen to raft, and no other attempts were noted during the study.

DISCUSSION

Despite unusual morphology and advanced development at birth, newborn *H. comes* seahorses behave in the plankton like most studied reef fish larvae. These tropical seahorses advect passively, without apparently behaving in ways that affect their dispersal trajectories, at ages one through four days old, following release from parent's brood pouches. Seahorses differ from other reef fish in adopting their planktonic phase later in ontogeny, after developing directly into juvenile-stage young inside fathers' brood pouches. While newborn seahorses were not observed to swim against local currents, they did exhibit complex behaviours that included burst-swimming associated with prey capture, daily ontogenetic development of orientation and responses to solar cues. These behaviours suggest that seahorses act to optimize feeding, perhaps associated with their unusually advanced ontogeny during the pelagic-stage, relative to most planktonic-phase reef fishes.

Vertical Position

Seahorses in this study showed slight ontogenetic shifts in depth distribution, but were usually observed near the surface. Opportunistic in situ observations confirm that newly released young of many marine organisms (Craik & Harvey 1987; Saborido-Rey et al. 2003; Strathmann 1990), including other species of seahorses, behave similarly, moving up to the surface after birth (*H. bargibanti*, S. Lourie, pers. comm., *H. guttulatus*, J. Curtis pers. comm., *H.comes* J. Anticamara pers. comm.). Moreover, at least four other species of seahorses (*Hippocampus abdominalis, H. mohnikei, H. guttulatus, H. spinosissimus*), ranging in size from newborn to sub-adults, have been captured from surface plankton tows (Hickford & Schiel 2003b; Kingsford & Choat 1985; Perez-Ruzafa et al. 2004; Vandendriessche et al. 2005), although both large and small individuals have also been found in oblique tows (Kanou & Kohno 2001).

It has been suggested that positioning near the surface may be important to move eggs and larvae of fishes and other marine invertebrates into water layers with optimal environmental conditions for development. Surface waters provide appropriate refugia from predators, favourable concentrations of prey, and optimal salinity or oxygen concentrations (Saborido-Rey et al. 2003; Strathmann 1985; Strathmann & Strathmann 1982). The development of gas bladders in seahorses has not be explicitly researched, but for other fishes and for seahorses (Woods 2000a), it is believed that young use initial contact with the surface to fill their gas bladders after birth. This behaviour is common in the larvae/juveniles of both physoclistous fishes (with closed gas bladders) like seahorses, and physostomous fishes (with gas bladders connected via a pneumatic duct to the esophagus) (Govoni & Hoss 2001; Zwerger et al. 2002).

We saw that *H. comes* young used short bouts of swimming to influence their position in the water column, but usually over only short distances (<1m) and by older (>Age 2) individuals exhibiting a flight response after contact with the surface. Theoretically, burst swimming has the potential to influence both depth distributions and dispersal trajectories, and to bring young in contact with settlement habitat (Fisher et al. 2005). However, *H. comes* achieved the greatest changes in depth via gradual descents, rather than burst swimming. Seahorses have large swim bladders that begin at the neck and extend over approximately one third of the length of the coelomic cavity (Bull & Koldewey 2002). For these weak swimmers, regulation of the swim bladder may be more influential than outright swimming, for controlling vertical position in the water column.

Swimming and Orientation

Our findings indicate that in the early portion of their pelagic phase, *H. comes* disperse in a largely passive manner without evidence of sustained swimming ability. They do, however, orient actively relative to their immediate surroundings via fin positioning and/or burst-swimming and the ability to orient upstream develops with age. Largely passive dispersal without regular sustained swimming may be a feasible strategy for species such as *H. comes* with a pelagic duration that is short relative to coral reef fishes and is more comparable to invertebrates (Sale & Kritzer 2003). Short dispersal periods are believed to evolve in systems where patches of suitable settlement habitat are found at low density (Strathmann 1990). In such systems, the cost of moving away from settlement habitat is high (Dytham 2003). *Hippocampus comes* settles predominantly into wild macroalgal beds, and less often on coral reefs (Morgan & Vincent 2007). These shallow communities form concentrically around land and atolls in tropical reef ecosystems and are rare relative to the intervening deepwater matrix. The limited swimming ability of seahorses relative to most other fishes may also "increase" the effective distance between patches if active translation towards patches is not physically or energetically feasible.

Our observations indicated that seahorses are capable of fine-scale orientation relative to items in the water column and that they engage in short spatial and temporal periods of burst-swimming to move away from threats or to capture prey. Unlike most other demersal fishes (Leis 2006), this swimming ability exists from the first days of the pelagic phase in *H. comes*. However, there was no evidence that newborns were effective swimmers with propulsion exceeding ambient current speeds. Swimming performance (speed) of larval fishes tends to be related to propulsive area, when measured as the area of body and fins, excluding head and gut (Fisher et al. 2000). Seahorses use non-body locomotion, where propulsion is generated only from the small surface area of the single undulating dorsal fin and two small pectoral fins (Blake 1976; Consi et al. 2001), versus lateral body flexion. Therefore, their horizontal translation will be slow relative to most perciform fishes. Other demersal fishes whose larvae exhibit non-perciform morphology such as clupeiform, gadiform and pleuronectiform fishes are also suspected to be less behaviourally capable than perciform taxa (Leis 2006). Non-body locomotion is well adapted for the benthic phase of seahorses' bipartite life history and for fishes that move slowly and precisely to feed and mate in obstacle-strewn environments such as macrophyte beds and coral reefs (Lindsey 1978).

Solar Cues

Temporal differences in the variance of seahorse bearings suggest orientation relative to solar cues. In aquatic systems, orientation to light occurs either by tracking the position of the sun directly, or by detecting underwater polarized light from the sun (Horvath & Varju 1995). The influence of light on fish behaviour is poorly understood, but sensitivity to polarization may aid migration (Schwassmann & Hasler 1964) or help to locate the sun during overcast conditions (Horvath & Varju 1995). In species such as cephalopods, sensitivity to polarized light has also been demonstrated to enhance feeding on transparent, polarized prey items (Shashar et al. 1998). For reef-associated fishes, sensitivity to polarization could be used during planktivory, schooling, courtship, spawning, and/or the maintenance of territories (Hawryshyn et al. 2003). The position of the sun should not however, provide information reliably associated with appropriate settlement habitat or reefs. For broadly dispersing taxa known to detect solar cues (e.g. crab megalopae, Shanks 1995), this sensory ability may also be useful for general navigation (e.g. across continental shelves) where target destinations are broad and little directional accuracy is required (Kingsford et al. 2002).

Seahorses, pomacentrids and grunts are amongst the few reef fish families that have exhibited behaviour in relation to solar cues (Kingsford et al. 2002; Leis et al. 2007; Quinn & Ogden 1984): other observed reef families have not shown this behaviour in the field (Leis & Carson-Ewart 2003). Pomacentrids were recently shown to have the most complex visual sensitivity to polarization known among vertebrates, which is thought to play an integral role in foraging, species-environment interactions and inter-/intraspecific interactions, in structurally complex habitat (Hawryshyn et al. 2003). Like damselfishes, seahorses inhabit three dimensionally complex macroalgal beds and coral reefs (Curtis & Vincent 2005; Foster & Vincent 2004a; Kendrick & Hyndes 2003; Morgan & Vincent 2007). It is possible that seahorses, as visual ambush predators (Muller & Osse 1984), could use polarized light to locate prey items from the water column. Similarly, ability to detect polarized light could be used in seahorses'complex courtship behaviours, that often includes changes in pigmentation and positioning relative to mates (Vincent 1995).

Foraging

In this study, we saw that early behavioural capacity and ontogeny, such as burst swimming and development of orientation, were likely to facilitate feeding. This evidence suggests that seahorse young require regular intake of food items during their pelagic phase. Feeding "on the run" , observed here, has been noted in other reef fishes (Leis & Carson-Ewart 1998) and is experimentally demonstrated to extend swimming duration (Leis & Clark 2004). Planktonic feeding is also characteristic of seahorse young reared ex situ (Woods 2000a), which need high prey densities for successful rearing: this has been attributed to low food conversion ratios in the absence of masticatory structures and a true differentiated stomach (Rauther 1925; Woods & Valentino 2003). We did not identify prey items taken by wild young, but in aquaculture, seahorses have been successfully reared on a sequence of feeds ranging from artemia and rotifers, through copepods to mysid shrimps (Wilson & Vincent 1998). While these items enable seahorse growth, they may not be representative of the taxonomy, diversity or caloric content of wild prey items.

Experimental Considerations

The behaviour of young in this study may have been affected by food availability and nutrition. We were careful to use only individuals that showed the ability to remain vertically positioned in the water column, maintain buoyancy in mid-water and orient to prey items. However, we observed increased impairment of these abilities in individuals older than 5 days. The gape size of seahorses aged 1-4 was substantially smaller than the mesh on holding cages, so should not have obstructed the entry of appropriately sized prey. In the wild, planktonic seahorses are found at extremely low densities, so are unlikely to have to compete with conspecifics for food. Food availability in cages may have been reduced through stocking density, particularly if prey could avoid cages or if cage location 20 cm above the bottom did not promote the entry of appropriate plankton. Other problems such as disease (e.g. Vibrio harveyi Tendencia 2004), or developmental defects associated with poor nutrition (e.g. lordosis, poor inflation of gas bladders, skeletal deformities etc., Menu et al. 1998; Nagano et al. 2007; Trotter et al. 2001) may also have impaired buoyancy regulation and orientation abilities.

Conclusions

This work represents a first exploration of how planktonic behaviour may influence the dispersal of newly released seahorses. The only other study that has examined the in situ behaviour of a reef fish early in development, showed that *Amblyglyphidodon curacao* was capable of directed swimming and at speeds comparable to ambient currents. This species has perciform morphology well adapted for propulsion, and focal subjects ranged from 11-15 days old, so were substantially older than seahorses observed here, but of comparable size (8-10mm) (Leis et al. 2007). Our field results provide a first corroboration for ex situ research which has shown that for approximately the first 50% of their pelagic phase, reef fishes young seldom swim at rates that substantially affect their advective trajectories (Fisher 2005). Since the behaviours of pelagic-stage fish vary widely under even different types of laboratory settings (e.g. performance in swimming flumes, versus undisturbed swimming (Fisher 2005; Fisher & Bellwood 2003), it will be important to ground-truth laboratory results in situ. Only when we have realistic performance inputs, observed under natural conditions (Leis et al. 2005), will it become possible to build models that reasonably predict patterns of population connectivity (Armsworth et al. 2001).

To extend our understanding of juvenile seahorse ecology, it would be useful to follow young for longer periods of time, on tides that carry them into open water and to depths where they have been found in ichthyoplankton tows (Chapter 2). The settlement window at the end of the planktonic phase is a crucial survivorship boundary for many reef fishes (Hoey & McCormick 2004; McCormick 1998; Searcy & Sponagule 2001), so understanding recruitment behaviour and interspecific interactions during this period could provide insight into mechanisms that regulate the structure of benthic populations. We also know little about the physiological abilities of seahorses during either planktonic or settled juvenile phases of the life history.

We suggest that future research with coral reef fishes should attempt to address the following challenging, but important issues - the effects of using: a) young from wild parents, b) young reared in variable temperature, current, or light regimes that are representative of the wild, versus static, controlled conditions, c) using young fed wild versus cultured prey items, d) only the largest, strongest or best performers in populations versus “average” performers (Clark et al. 2005) and e) young that span a sufficiently wide size/age range to document behavioural ontogeny throughout the complete pelagic phase, not just prior to settlement, or immediately following birth (Leis & McCormick 2002). Particularly critical will be identifying the onset of behaviours that affect dispersal trajectories (Cowen et al. 2006), in situ.

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Table 1. Mean bearing of young and instantaneous downstream current direction at the beginning (t = 0) and the end (t = 15) of follows, where t represents time in minutes after young exited the release box. Difference gives the absolute degree difference between mean bearing and mean current direction. Test statistics are provided for the circular chi-squared goodness of fit test (χ^2), the Watson-Williams F test (F values) and p (χ^2), the circular chi-squared probability of rejecting the null hypothesis of no difference in distribution between bearing and current direction for t = 0 (at release) and t = 15 (end of observations) at each age, and p (WW) the probability of no difference in mean angle. Chi-squared tests where groups did not meet the assumption of ≥ 5 individuals per class are indicated by ~. Significance is indicated for p<0.05 by * and for p<0.01 by **.

			t = 0				
Age	**Mean bearing**	**Mean Current**	**Difference**	χ^2	**F**	***p*** **(χ^2)**	***p*** **(WW)**
1 (n = 12)	226.2	68.8	157.5	16.1	24.1	0.185	**<0.001
2 (n = 18)	218.2	63.5	155.1	30.7~	45.5	*0.022~	**<0.001
3 (n = 17)	265.2	66.6	161.4	32.0~	14.6	**0.006~	**<0.001
4 (n = 16)	296.5	62.1	125.5	29.0	29.4	0.066~	**<0.001
			t = 15				
1 (n = 12)	92.6	61.7	30.9	12.3	1.2	0.34	0.29
2 (n = 18)	107.9	67.4	40.5	18.2	3.9	0.31~	0.06
3 (n = 17)	35.7	62.2	26.6	20.1	0.9	0.17~	0.36
4 (n = 16)	47.8	67.2	19.4	22.3	0.2	0.07	0.63

Table 2. Multiple post-hoc Wallraff test results showing differences in the angular dispersion of all (uncorrelated) bearings of *Hippocampus comes* young, aged 1 day (Age 1) through 4 days old (Age 4). U is the value of the Mann-Whitney test statistic used in Wallraff tests (Zar 1999), p values give the probability of no difference in angular distance from the mean angle between day ages; Holm-Bonferonni significance (α = 0.05) is indicated by an asterix (*).

Age, a vs b	**n_a**	**n_b**	**U**	***p***	**Holm-Bonferroni adjusted α**
Age 1 vs 2	331	473	72589.0	0.079	0.025
Age 1 vs 3	331	506	66028.0	<0.001*	0.008
Age 1 vs 4	331	392	49706.0	<0.001*	0.010
Age 2 vs 3	473	506	106042	0.002*	0.017
Age 2 vs 4	437	392	80674.0	<0.001*	0.013
Age 3 vs 4	506	392	97719.0	0.705	0.05

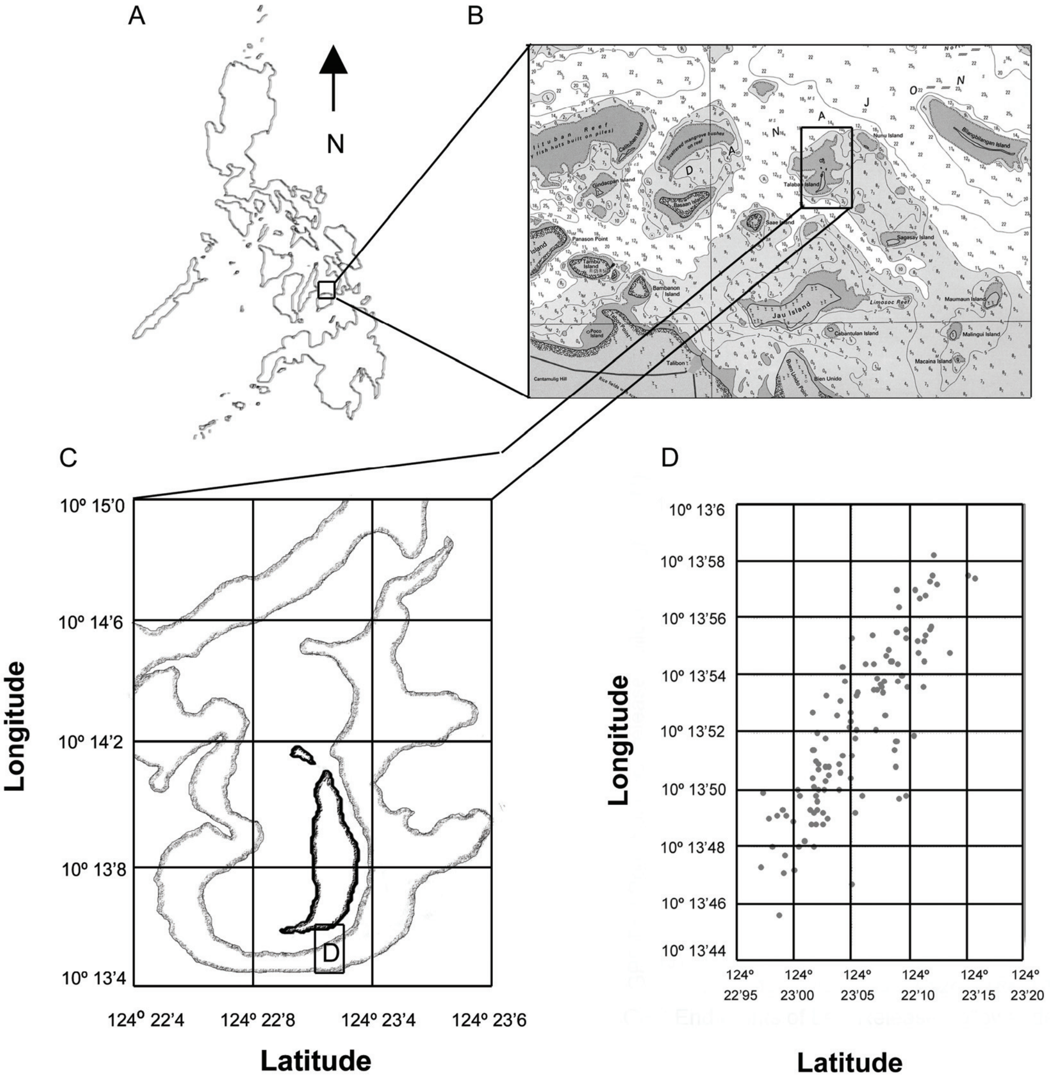

Figure 1. Location of study site in A) Bohol province, central Philippines; B) on the northern portion of the Danajon Bank, a double barrier reef system traversing the north coast of Bohol province; and C) at Cataban Island. The study area is shown on map C) as the inset rectangle (D) on the south-east corner of Cataban Island corresponding to Fig. D), which shows the endpoint of all focal observations. All young were released from the same location (10˚13'505 N, 124˚ 23'030 E).

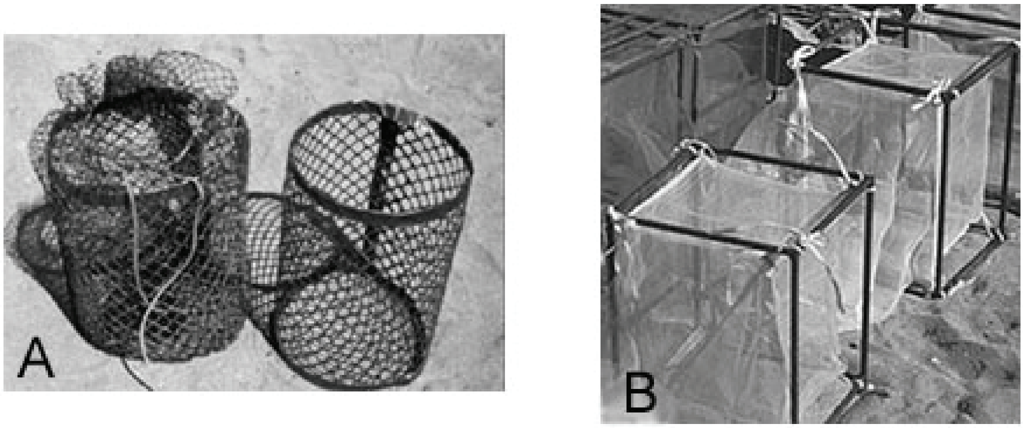

Figure 2. Cages for holding A) brooding male seahorses, and B) newborn seahorse young. A) Cylindrical cages were made of large diameter plastic mesh, encased in smaller mesh bag that prevented the escape of males, but allowed the passage of prey items. Drawstring opening at the top of mesh bags allowed easy entry or removal of males. B) Rectangular double thickness mesh bags tied to rebar frames were used to hold young seahorses. Material was gathered and closed laterally on one side of cages which, 1) allowed squeeze bottles to be easily inserted and maneuvered inside cage to gather small and positively buoyant young, 2) prevented the suffocation of young in mesh folds which occurred when folds were located on the upper surface of cages, and 3) allowed simple underwater transport of young inside low volume mesh bags, easily detached from rebar frames.

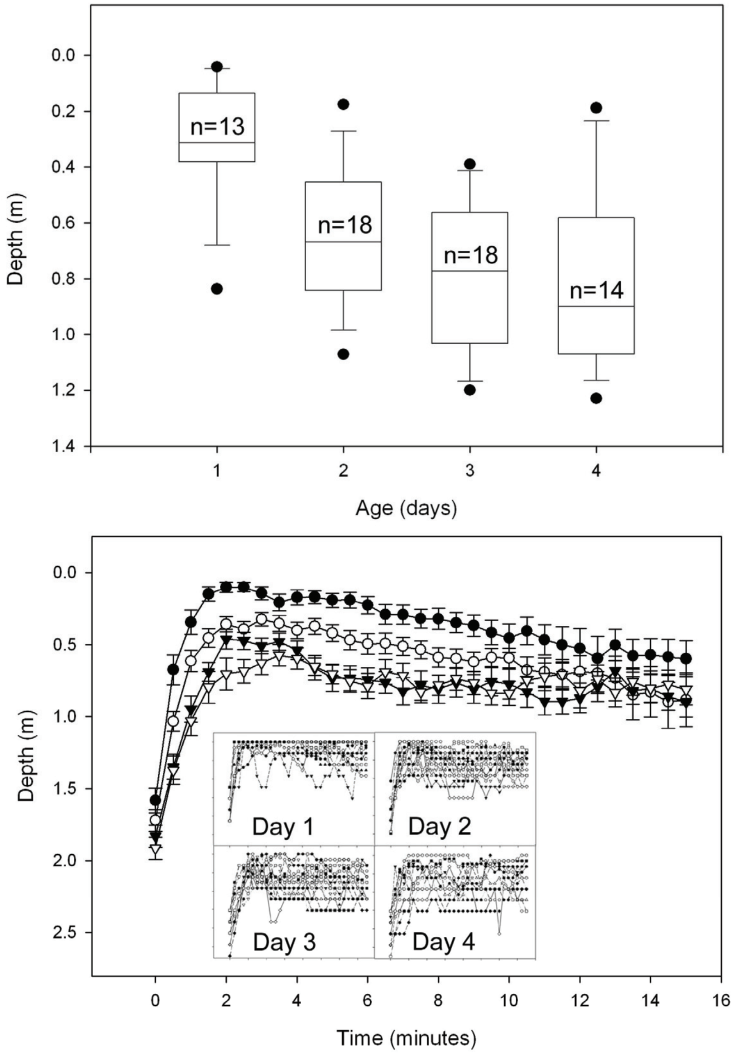

Figure 3. Box plots and depth trajectories for tiger tail seahorse (*Hippocampus comes*) young followed on days 1-4 post-release, from the same location on Cataban Island reef flat (10˚13’505 N, 124˚ 23’030 E). In the upper figure, the floor of box plots denote the 25th percentile of mean depths, the centre line the median, the ceiling the 75th percentile, whiskers the 10th and 90th percentiles and points show outliers. The lower figure shows the overall mean depth trajectory across individuals (sample size given in box plots) for Ages 1 ●, 2 ○, 3 ▲ and 4 Δ. Error bars give the standard error of the mean depth for a given time, within a given age. Inset boxes illustrate individual trajectories by age, using the same axes as the lower figure.

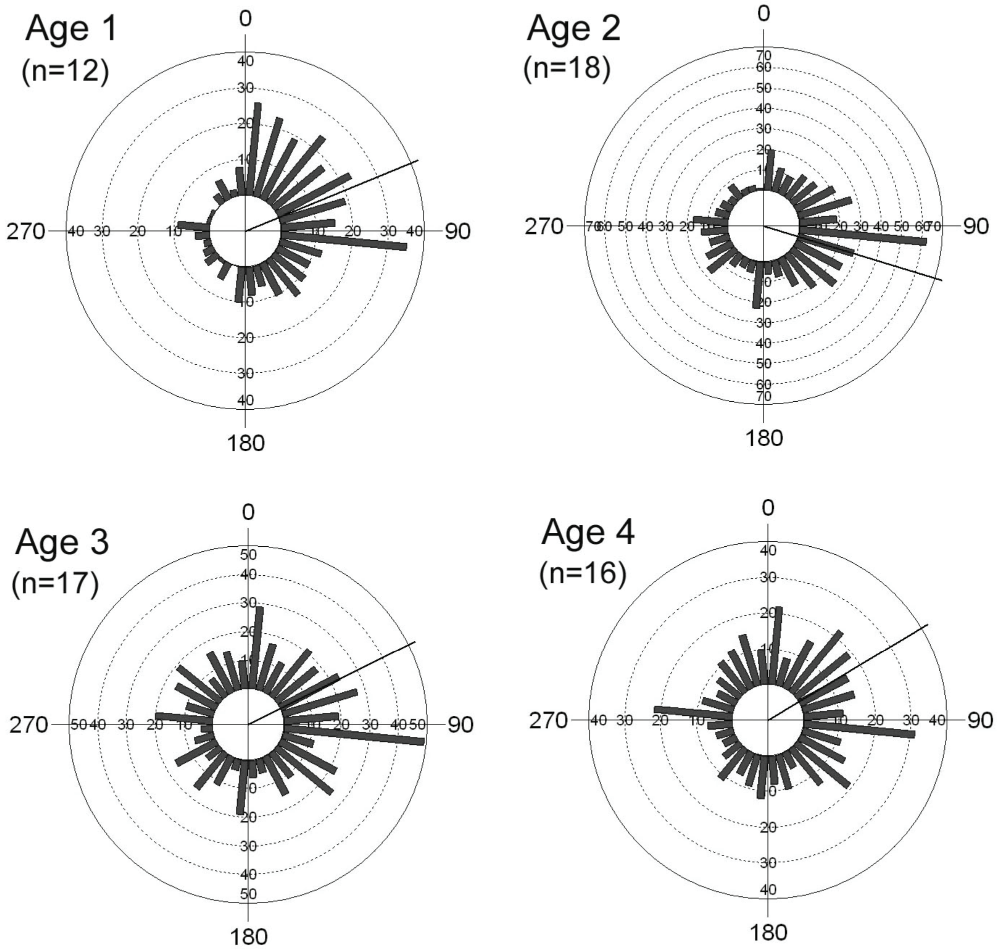

Figure 4. Circular frequency distributions of instantaneous in situ swimming bearings (Day 1: n = 331, Day 2: n = 473, Day 3: n = 506, Day 4: n = 392) for newborn tiger tail seahorses (*Hippocampus comes*) aged 1-4 days after birth (release). Numbers on dashed concentric circles give the total frequency with which bearings were observed. Straight lines extending beyond the circumference of plots, give the mean vector bearing (μ) for each day age.

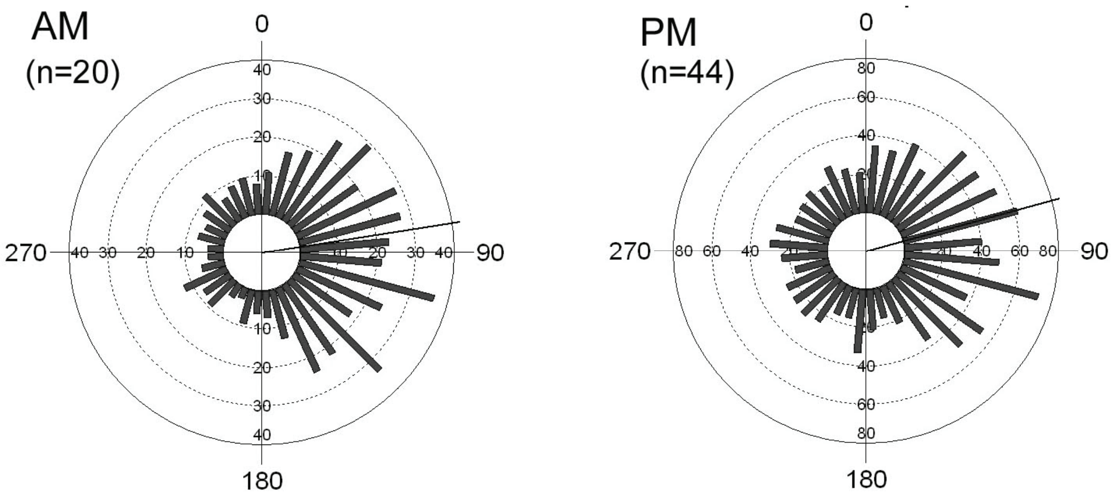

Figure 5. In situ swimming bearings of newborn *H. comes* during morning (n = 528 bearings, n = 20 individuals) and afternoon (n = 1174 bearings, n = 44 individuals) focal observations on the Danajon Bank, Philippines. Numbers on dashed concentric circles give the relative frequency with which particular bearings were observed. Lines extending from the centre of distributions to the perimeter of plots indicate the mean vector direction of all bearings. The length of the mean vector (r, not shown), is an indication of bearing concentration where 0 = maximum dispersion, 1 = lack of dispersion. r_{am}= 0.379, r_{pm}= 0.232.

LINKING STATEMENT II

In Chapter 1, I showed that seahorse young released from natal reefs rise rapidly to positions near the surface, increasing their capacity to orient within the water column during the first days following birth. Despite the ability to exercise complex behaviour such as burst-swimming associated with prey capture, there was no evidence that newborn seahorses swam against ambient current: rather, they advected passively. In this chapter, I quantify the abundance and distribution of young in the plankton, assess how long individuals remain pelagic, and consider whether rafting might influence transport.

Here, I combined ichthyoplankton research with preliminary oceanographic information to generate the first estimates of potential dispersal distances between demographically linked populations of tropical seahorses. This information is important to evaluate the scale of connectivity among populations in the central Philippines. Findings are relevant to the structure of metapopulations, the placement of marine reserves, replenishment of fishing grounds under present heavy rates of exploitation, and conservation incentives for fishing communities. This approach may be appropriate for preliminary scaling of management in other data-poor taxa.

CHAPTER 2

PLANKTONIC DISPERSAL OF TROPICAL SEAHORSES (*Hippocampus spinosissimus* Weber, 1913 and*Hippocampus comes* Cantor, 1850).

ABSTRACT

Most reef fish have a bipartite life history, comprised of a mobile planktonic phase, followed by a sedentary benthic adult phase. Because seahorses are small, demersal and develop directly, there has been conjecture that they lack a pelagic phase. Here, we asked whether tropical seahorses have a planktonic phase and if so, how time of day, depth and availability of floating debris relate to the size and abundance of young in the plankton. Neuston (surface) and oblique (mid-water) tows were undertaken at Sagasa Island in the central Philippines during the day and at night. We found two species of seahorses, both at low densities; deeper-water *Hippocampus spinosissimus* Weber 1913 was about 5X more abundant than the shallow-dwelling *Hippocampus comes* Cantor, 1850. *Hippocampus spinosissimus* young, which ranged in size from 6.4-23.7 mm standard length, were more abundant by night, and largest in oblique tows. *Hippocampus comes* young spanned 9.5-16.8 mm and were most abundant in oblique tows. Despite the presence of floating debris in most tows, there was no strong evidence that seahorses were using rafting as a dispersal mechanism. Planktonic duration was estimated to fall between 8-10 days for *H. spinosissimus* and 5-10 days for *H. comes*, corresponding to maximum dispersal distances ranging between ca.12-210 km depending on lunar phase and currents. This is a short planktonic phase relative to other small demersal teleosts and more comparable to the planktonic phase of invertebrates. Furthermore, it is consistent with theory predicting shorter dispersal periods in marine organisms with weak swimming ability and from patchy habitat versus continuous coastlines.

INTRODUCTION

Over 95 % of fishes on coral reefs have a two-phase, or bipartite, life history, with important implications for population dynamics on both evolutionary and demographic scales (Leis 1991). In the first phase, propagules (unfertilized gametes, fertilized eggs or small juveniles) move into the water column where they spend from a few days to months in open ocean waters, typically dispersing over distances on the scale of 10s-100s of km (Cowen et al. 2006; Wellington & Victor 1989). In the second phase of their life history, recruits settle to the benthos to undertake a largely sedentary adult existence, often far from natal reefs. For indirectly developing fishes, the transition from the water column to the seabed often coincides with metamorphosis, when larvae suited to a planktonic existence undergo subtle or dramatic morphological changes that modify the body to the juvenile form (McCormick et al. 2002). Taxa as diverse as echinoids, crustaceans and corals all possess planktonic and benthic phases, suggesting that there are broad evolutionary advantages conferred by this two-phase strategy (Bonhomme & Planes 2000).

Interest in the planktonic phase (also called the pelagic period) of marine life histories arises from the recognition that dispersal patterns structure connectivity and are therefore an important determinant of population dynamics. Although many marine populations are genetically open - sending/receiving propagules from another population (sensu Mora & Sale 2002) - over evolutionary time scales (Johnson 2005), both direct captures and modeling have recently shown that reef fish populations are more “closed” - having a greater proportion of young retained - than was previously thought (Cowen et al. 2006; Jones et al. 1999; Swearer et al. 1999; Swearer et al. 2002). There is also recognition that the dichotomy of open/closed populations is largely dependent on spatial and temporal scales of reference which should be clearly defined (Johnson 2005; Mora & Sale 2002).The dispersal patterns of populations are most accurately described as dispersal kernels, which provide a probability distribution of destinations from a point of origin in a single unit of time (Chesson & Lee 2005; Kinlan et al. 2005; Steneck 2006). Nonetheless, dispersal distances and durations may vary substantially across time and space based on conditions such as location and season (Bay et al. 2006).

Many factors affect the dispersal trajectories of propagules from natal reefs. Total distances traveled are governed by physical oceanographic processes and their interaction with the behaviour of propagules. Particularly when they are young and poorly developed, reef fish larvae are subject to physical processes. Oceanic features that can either enhance dispersal or local retention include advection, diffusion, tidal currents, mesoscale eddies, oceanographic gyres, frontal systems, Taylor caps, temperature, and wind forcing at the time of release (Bradbury & Snelgrove 2001; Cowen et al. 2000; Green & Fisher 2004). The release behaviour of adults may also be timed to coincide with oceanographic events. Once in the water column, many reef fish families are strong swimmers, capable of achieving speeds that match or exceed average ambient currents, particularly close to settlement (Fisher 2005; Fisher et al. 2000; Leis & Carson-Ewart 1997; Stobutzki 1998; Stobutzki & Bellwood 1997). Late-stage larval reef fish also exhibit substantial behavioural capacity in terms of their orientation (Leis & Carson-Ewart 2003; Leis et al. 1996; Stobutzki & Bellwood 1998) and sensory capabilities (Job & Bellwood 2000; Tolimieri et al. 2000). Mechanisms such as rafting also have the potential to mediate movement, either during the primary dispersal of propagules or in secondary dispersal of larger juveniles and adults. For dispersing young, the ability to raft on floating matter provides a means to effectively prolong planktonic duration beyond the larval period or to travel distances that are greater than could be achieved by swimming alone (Worcester 1994).

Most marine reef fishes undertake planktonic dispersal, and their young are characterised by a suite of traits adapted to life in the plankton. Many of these characteristics are not seen in seahorses, so there has been conjecture that seahorses could be reef fishes without a typical pelagic phase (Barlow 1981; Bonhomme & Planes 2000). Most tropical coral reef fish species: a) undergo metamorphosis in the plankton; b) are morphologically perciform (perch-like); c) have young that attain behavioural competency at the end of their planktonic phase; d) are strong swimmers near settlement, relative to both ambient currents and their temperate counterparts (Leis & Carson-Ewart 1997); and e) are transparent to reduce the risk of predation (Johnsen 2001). In contrast, seahorses: 1. exhibit extensive parental care in which young undergo direct development in the brood pouch of males prior to release; 2. have non-perciform morphology, in keeping with temperate larvae from well-studied fish taxa that do not occupy reefs as adults (e.g. Clupeiformes, Gadiformes, Pleuronectiformes) (Leis & McCormick 2002); 3. release young that are capable of grasping with their prehensile tails within hours after birth in appropriate settlement habitat (S.K.M., unpublished data); 4. are likely to exhibit poor swimming abilities relative to other reef fish young; 5. are pigmented upon release and become more heavily coloured within days of release (Choo & Liew 2006; S.K.M., unpublished data).

Objectives

The aim of this research was to examine the in situ dispersal of tropical seahorses, focusing research on an area of known seahorse abundance in the central Philippines. We investigated dispersal indirectly because small brood sizes, depleted adult densities and challenges using otoliths to age animals, precluded direct tracking (Do et al. 2006; Vincent et al. 2007). Specifically, we asked a) whether tropical seahorses have a planktonic phase; b) whether time of day, depth and distance from shore had an effect on the size and abundance of seahorse young in the plankton; c) whether juvenile seahorse abundance is related to floating debris suitable to mediate dispersal via rafting; and d) the potential duration and range of dispersal. The unusual morphology of seahorses provides the opportunity to probe the ubiquity of bipartite marine life histories. These data will also help to inform scales of demographic connectivity needed for conservation and management of these heavily fished populations.

METHODS

Study Site and Sampling

Research was undertaken at Sagasa Island (10°12.05’N, 124°.75’E) from November 2002 to January 2003, in Bien Unido municipality, Bohol province, central Philippines (Fig. 1). Sagasa Island is part of the Danajon Bank, which stretches across the north and west shores of Bohol province and is the only double barrier reef system in the Philippines. The bank supports two main biotic communities: 4000 ha of mangrove forest and greater than 500 ha of seagrass beds at depths from 0-3 m (Green et al. 2000). Other reef zones include macroalgal beds and patch reefs with corals tolerant of disturbance, seasonal fluctuations in freshwater input, and moderate suspended sediment (e.g. *Porites* spp., *Seriatopora* spp., *Montipora* spp.). Contiguous swathes of higher diversity reef occur in offshore areas and well flushed regions with low turbidity. The Danajon Bank is densely inhabited and heavily fished, often using illegal gears that degrade habitat (Marcus et al. 2007).

Ichthyoplankton tows were conducted haphazardly to the northwest and southeast of Sagasa Island in areas sanctioned by the local community (Fig. 1). All ichthyoplankton tows (n = 244) used a standard ichthyoplankton net with a 1.3 m diameter mouth and 0.3 mm Nytex™ mesh. The net was fitted with a standard General Oceanics 1030R flowmeter to measure the volume of water sampled. Tows were stratified by time of day (day, night) and sampling depth (shallow/neuston, deep/oblique). Day tows were done in full daylight between 11:30 and 16:30 and night tows in complete darkness between 01:30 and 05:30. Shallow tows were centred at 0.5 m, and deep tows were centred at 5.0 m, which was approximately half way between the surface and the 9-10 m bottom. For each tow, the net was pulled at a mean ± SE speed of 1.6 ± 0.025 km hr^{-1} for 15 minutes (n = 240). Individual tows filtered 555.9 ± 8.6 m^3 (n = 240) of water, ranging between 162.8 m^3 and 1079.8 m^3.

Seahorses were hand-picked from ichthyoplankton samples and fixed in 95 % ethanol in individual microcentrifuge tubes fitted with O-ring seals. Floating debris (both organic and inorganic) was sun-dried in the field, then air-dried at room temperature in a laboratory for 2 weeks to standardize moisture content prior to weighing by digital balance.

To measure specimens, young were photographed next to a ruler using a digital camera mounted on a Leica™ dissecting microscope at magnifications ranging from X 16 to X 50. Contorted individuals were lightly pressed between two layers of Plexiglas and measured using the digital imaging program ImageJ available at http://rsb.info.nih.gov/ij/. Curved standard length (SLc) was measured as the combined head length (HL), trunk length (TrL) and tail length (TaL) following trunk and tail curves, as per Lourie (2003).

Study Species

Hippocampus spinosissimus Weber 1913, the hedgehog seahorse, is a deep water seahorse that is widely distributed from the Indian subcontinent (Sri Lanka) throughout South-East Asia (Malaysia, Singapore, Indonesia, Vietnam, Taiwan) and into Australasia (Australia, Torres Strait) (Lourie et al. 2004). In the central Philippines, *H. spinosissimus* occupies sandy environments at depths of 8-70+ m where adults use holdfasts that include single or small patches of ascidians, hexacorals, submerged branches, sponges and hammer shells (Morgan & Panes 2007). In the study area, compressor divers started to target local populations of this species in 2003, fishing mainly for adults (S.K.M., unpublished data).

In contrast, the tiger tail seahorse *Hippocampus comes* Cantor, 1850, inhabits shallow marine waters from 0.5-20 m and is found mainly in the Philippines, although there have been confirmed sightings in Indonesia, Malaysia, Singapore, Thailand and Vietnam (Lourie et al. 2004). Within the Philippines, *H. comes* is found in most provinces, with highest densities in the centre of the archipelago. *Hippocampus comes* uses finger corals, branching sponges, kelp and seagrass (*Enhalus acoroides*) as holdfasts (Morgan & Vincent 2007; Perante et al. 2002). Distinctive morphological features include adults often with a yellow and black striped dorsal surface, a low coronet with 5 points, double cheek spines, and a prominent nose spine (Lourie et al. 2004). There is an active artisanal fishery for *H. comes* in Bohol. Adults are dried and sold as ingredients for traditional medicine and young are sold alive into the aquarium trade.

Based on observed, inferred or suspected declines of 30-50 %, both *H. spinosissimus* (VU A4cd ver 3.1 (2001)) and *H. comes* (VU A2cd ver 3.1 (2001)) are listed as Vulnerable on the IUCN (World Conservation Union) Red List of Threatened Species.

Growth Data

Previous research on *H. spinosissimus* has shown that it is not possible to obtain accurate age counts on either a daily or annual basis using otolith banding (Do et al. 2006); the same is likely to be true for its sympatric congener *H. comes*. Instead, as suggested by Do et al. (2006), we estimated pelagic larval duration by using size data from seahorse young reared under ex situ conditions to estimate the ages of individuals from plankton tows. Such data are believed to provide reasonable proxies for in situ vital rates (Curtis & Vincent 2006).

Growth rates for both *H. spinosissimus* and *H. comes* were estimated from best available data for *H. comes,* which included published (Job et al. 2006) and unpublished data provided by Dr. S. K. Truong of the Vietnamese Institute of Oceanography at Nha Trang, Vietnam (see Appendix I for culturing information). In both studies, animals were reared in temperatures similar to ambient conditions at our field site and were fed prey readily available in situ. Ex situ growth rates are not presently available for juvenile *H. spinosissimus*. Growth of another, similarly-sized sympatric congener, *H. kuda* (Lsc(mm) = 1.53*age(days) + 10.2 mm) (Job et al. 2002), was similar to the rates we used, when *H. kuda* were grown on Selco-enriched *Artemia* . This suggests that it is reasonable to assume that growth of morphologically comparable congeners, reared under similar conditions, is likely to be consistent.

Drifters

A model 115 Lagrangian drifter buoy from Brightwaters Instrument Corporation was used to track current flows sixteen times in October and November of 2002. Each month, the surface drifter was released over two full tidal cycles corresponding to both a flood tide followed by an ebb tide ("Flood") and, an ebb tide followed by a flood tide ("Ebb"), during both spring tides (new moon, full moon) and neap tides (first quarter, last quarter). Tracks began on a slack tide in a marine sanctuary off Cataban Island (< 5 km from Sagasa Island), inhabited by both *H. spinosissimus* and *H. comes*. From an accompanying boat, GPS fixes of drifters were taken every 15 minutes and, once an hour, a hand-held Niskin bottle was used to sample water temperature to 0.1° Celcius at 1 m intervals between the surface and 5 m. Latitude and longitude values were used to calculate currents speeds. Frequent boat traffic and interest in the drifter by most artisanal fishers precluded the possibility of multi-day tracks without drifter supervision.

Planktonic Duration and Dispersal Distances

To explore possible dispersal distances in this complex reef-archipelago system, we modeled two dispersal scenarios. In the first, we assumed that maximum dispersal would occur when seahorses traveled in straight lines akin to dispersal via longshore flow, at speeds corresponding to the total distance traveled by drifters, per unit time. We called this movement "unidirectional flow", which corresponded to maximum dispersal potential. In a second scenario, we assumed that dispersal may be substantially less in the eddying currents among islands and calculated a net speed traveled corresponding to the straight line distance moved by drifters between the start and end of tracks, per unit time. We called this displacement “net flow”, which corresponded to minimum dispersal potential. Both types of movement were calculated for each drifter track, then grouped by spring and neap tides and fit to symmetrical sine curves using Sigmaplot™, representing average rates of unidirectional or net current movement (km hr^{-1}) at different phases of the moon, using the formula;

$$f(x) = (y_0 + aSIN(\frac{2\prod x}{b}) + c) + d \tag{Eq. 1}$$

Where a = amplitude, x = fraction of a week, b = period, c = constant and d was a vertical translation term.

Seahorses mainly drift passively in their early pelagic phase (Chapter 1) and are poor swimmers relative to other teleost fishes because they generate propulsion only from weak dorsal fin swimming (Blake 1980). The water column did not exhibit temperature differences often associated with depth-stratified current flows: measurements at 2 m intervals showed temperatures uniform within ± 1.5° C from the surface to the bottom of the deepest 22 m channels. Therefore, we invoked simplifying, but feasible assumptions that: a) seahorse young do not influence their horizontal trajectories through directional movement; and b) current speed and direction is consistent throughout the water column.

The maximum and minimum pelagic duration in days (PD) was derived by back-calculating ages from the sizes of the largest planktonic and smallest settled individuals, based on ex situ growth rates. Dispersal distances were then calculated with the following inferences:

- Maximum dispersal distances were derived by summing daily dispersal distances in unidirectional flow on spring tides, over the maximum pelagic period, corresponding to the smallest settled young.

- Minimum distances were derived by summing daily dispersal distances in net flow on neap tides, over the minimum pelagic period, corresponding to the largest planktonic individuals.

When calculating dispersal, we centred the midpoint of inferred pelagic duration at local optima associated with either spring or neap tides. Potential dispersal distances were then calculated by integrating symmetrically across current speeds to either side of optima. For example, for an animal with a pelagic duration of 5 days, dispersing on a spring tide, in unidirectional flow, the disperser was assumed to move at maximum spring tide currents on day 3 of its pelagic period, at current speeds that were slightly slower on days 2 and 4, and that were yet slower on days 1 and 5.

Data Analysis

For tows, abundance was collected in the form of counts. These data were strongly right-skewed, and neither log, nor square root transformation achieved normality, so they were rank transformed (Potvin & Roff 1993). To test spatial and temporal determinants of size and abundance, we used two-way analysis of variance, with time of day and depth as fixed factors on length and ranked counts respectively (Conover & Iman 1981).

We tested for evidence that seahorse young use floating debris for rafting two ways. First, we examined differences in biomass among tows with and without seahorses. We also examined whether biomass of floating debris was correlated with seahorse abundance per tow. Because many tows did not capture seahorses (and therefore may have represented water strata fundamentally unsuitable to seahorse young), we also tested whether there was any relationship between total debris/organic debris and seahorse abundance, for only tows that contained seahorses.

Comparative analysis of pelagic duration versus total length were made by querying FishBase (URL:http://www.fishbase.org) and by compiling literature sources for tropical reef species that guard or bear live young, from waters ≥ 25 ˚C, comparable to the Philippines.

Data were stored in an MS Access™ database and analysed using SPSS 11.5™ and Sigmaplot 8.0™.

RESULTS

Abundance – Species and Density

We found two species of seahorses in tows, both at low densities. Seahorses were captured in 21.3 % (n = 52) of tows with 1 - 6 individuals captured per tow (Fig. 2). Overall, we found 84 seahorses in 244 tows, of which 87 % (n = 73) were identified as *H. spinosissimus* and 13 % (n = 11) as *H. comes*. Young were differentiated based on patterns of spination and body proportions. Spination was dichotomous, based on prominence of spines at the intersection of dorsal and superior plates, superior and lateral plates, and lateral and inferior plates. In one group, animals had large spines at body segments 1, 4, 7 and 11 and in the other, at body segments 1, 4, 6, 8 and 11. These morphological patterns were mapped onto, and matched, patterns of prominent spines seen in adult *H. spinosissimus* and *H. comes* (Lourie et al. 2004). Differences in body proportions among the two groups of young also matched visible differences in the ratio of snout length:head length and trunk length:tail length between adult *H. spinosissimus* and *H. comes.*

Abundance varied between the two species and by type of tow. Overall, mean ± SE density for all tows was $6.03 \times 10^{-4} \pm 9.32 \times 10^{-5}$ individuals m^{-3}. *Hippocampus spinosissimus* were over 5 times more abundant in the plankton than *H. comes*, although both were found at very low densities (1 individual per 2000 m^3 and slightly less than 1 individual per 10 000 m^3 respectively) (Table 1) (Fig. 3). Tows with >4 individuals per tow occurred only at night, and the majority of tows contained no seahorses (n = 192) (Fig. 2). *H. spinosissimus* young were twice as dense in night tows (n = 51) as they were in day tows (n = 21), but there was no evidence that densities differed between the surface and midwater (Table 2, Fig. 3). In contrast, >80 % of *H. comes* young were found in deep tows (n = 9), but densities did not fluctuate in relation to time of day (Table 2). Seahorse density was not related to distance from land (Sagasa Island) for either *H. spinosissimus* (Spearman's rank correlation, $r_{s\,(2,242)} = 0.056$, p = 0.380) or for *H .comes* (Spearman's rank correlation, $r_{s\,(2,242)} = 0.036$, p = 0.576).

Abundance - Size

Seahorse size varied by species, and in *H. spinosissimus*, by depth. *H. spinosissimus* sizes were right-skewed with few large individuals in the length distribution (Fig. 4). *Hippocampus spinosissimus* young were significantly smaller than *H. comes* (independent sample t-test, t = 4.232, p<0.001, df = 82), averaging 10.0 mm and 13.6 mm SLc, respectively (Table 1). Minimum sizes reflected similar differences, where the smallest *H. spinosissimus* measured 6.4 mm and the smallest *H. comes* was 9.5 mm SLc. *Hippocampus spinosissimus*, ranged up to 23.6 mm, while *H. comes* only reached 16.8 mm; hence apparent planktonic sizes spanned 17.2 mm in *H. spinosissimus* and only 7.3 mm in *H. comes* (Table 1). There was strong evidence that *H. spinosissimus* in the neuston were smaller than conspecifics inhabiting the water column (Table 2).

Rafting

There was no evidence that the amount of floating matter was related to the abundance of planktonic young. Tows with seahorses contained on average, less biomass (mean ± SE of 4.1 ± 1.5 g) than tows without seahorses (9.0 ± 2.8 g), but these differences were not statistically significant (Mann-Whitney test, U = 4719.5, p = 0.47, n = 127). For both *H. spinosissimus* and *H .comes*, there were no meaningful relationships between seahorse abundance and either the biomass of total debris or organic debris (Table 3). Similarly, for only tows that contained seahorses, there was no correlation between floating debris and abundances of either *H. spinosissimus* or *H. comes* (Table 3). Greater than 95 % of floating debris captured in tows was comprised of seagrass fragments (*Thalassia hemprichii)*. Organic matter also included fragments of other seagrasses (*Enhalus acoroides*, *Syringodium* spp.), mangrove matter (leaves and propagules) and coconut husks. Non-organic debris made up 1.5 % of the total and was plastic; with 90 % from fishing lines/floats and 10 % from shopping bags, toys and shoes.

Growth Rates and Planktonic Duration

Growth rates for *H. comes* young were best fit using two straight lines representing: a) growth between birth and 3 weeks, and b) growth from 3 weeks to 2 months. Other studies have also shown that young seahorses exhibit growth inflection points (Boisseau 1967; Choo & Liew 2006). We tried fitting a series of logarithmic and power functions, but these implied improbably rapid growth immediately after release (4 mm day^{-1}), not consistent with observations at rearing facilities (Dr. S. K. Truong, pers. comm.), and more than double the growth seen in other species (Wilson & Vincent 1998).

Growth rate was best described by the function;

$$y = x * m + y_0 \qquad \text{(Eq. 2)}$$

where y is SLc (mm), of young at a given age, x, in days. The rate of change of standard length with time is described by m, the slope of the line, and y_0 is length at birth (mm).

The two data sets we used for *H. comes* showed differences in growth at ages >3 weeks, but similar rates between release and 3 weeks. Therefore, we used all data available from release to 21 days to plot a predictive relationship for age as a function of SLc (Fig. 5) giving;

SLc (mm) = age (days)*1.80 + 8.00 (mm) (Eq. 3)

We used this model to infer minimum and maximum pelagic durations of *H. spinosissimus* and *H. comes* (Table 4). Minimum pelagic durations were estimated for both species from the largest planktonic individuals in tows and corresponded to 8.7 days for *H. spinosissimus* (23.6 mm) and to 4.9 days for *H. comes* (16.8 mm). Conservative estimates of maximum pelagic duration were calculated from the size of the smallest benthic individuals, which we assumed to be just post-settlement (Chapter 3). For *H. comes*, these benthic individuals are larger than any size classes observed in the plankton, since we assumed that our limited sample sizes may not have captured the largest planktonic individuals. There are no field data for size at settlement for *H. spinosissimus*, so we used the size of the smallest settled *H. comes* (26.7 mm) as a reasonable proxy for maximum pelagic duration for both species. A SLc of 26.7 mm corresponded to a maximum pelagic duration of 10.4 days for both species.Congener *H. kuda*, reared ex situ in temperatures comparable to field conditions, settles at a similar size (22.4 mm) (Choo & Liew 2006). The mean ± SE pelagic duration of all *H. spinosissimus* at their time of capture was 1.2 ± 0.2 days, and of all *H. comes* was 3.1 ± 0.5 days.

For context relative to reef fishes, we examined the pelagic duration of tropical demersal fishes exhibiting guarding/live-bearing behavior. There was a significant relationship between body size and maximum pelagic duration (Spearman rank correlation, $r_s = 0.43$, $p = 0.03$, $n = 24$) (Fig. 6). Tropical seahorses were a notable exception, lying on the lower 95 % prediction interval of this relationship. The only other species outside the prediction interval was *Acanthochromis polyacanthus*, a species with no pelagic phase (Fig. 6).

Drifters and Dispersal Distance

Lagrangian drifter tracks of unidirectional flow on the four phases of the moon differed significantly in their speeds (one way ANOVA, $p<0.001$, $F = 17.35$, $df = 3$, $n = 16$). Post-hoc Tukey tests ($\alpha = 0.05$) indicated that differences were significant between spring and neap tides (Fig. 7). Tidal flow on spring tides moved at a rate of 0.94 ± 0.08 (SE) km hr^{-1}, more than twice as quickly as neap tides (0.40 ± 0.04 km hr^{-1}) (Fig. 7, Fig. 8). Differences in current speed between spring and neap tides for net displacement were not as large as for unidirectional movement, but ranged from a spring high of 0.30 ± 0.03 km hr^{-1} to a neap low of 0.14 ± 0.05 km hr^{-1}.

Formulae for unidirectional and net flow, respectively, were:

$$f(x)_{unidirectional} = (-0.1408 + 1.97SIN(\frac{2\Pi x}{2.0}) + 4.6228) + 0.809 \qquad \text{(Eq. 4)}$$

$$f(x)_{net} = (-0.021 + 0.04SIN(\frac{2\Pi x}{2.0}) + 4.9) + 0.239 \qquad \text{(Eq. 5)}$$

(Eq. 4, nonlinear $regression_{unidirectional}$, n = 39, F = 25.68, $R^2 = 0.68$, $p<0.0001$; Eq. 5, nonlinear $regression_{net}$, n = 39, F = 6.02, $R^2 = 0.33$, p = 0.002). Calculations indicated that potential dispersal distances range more than an order of magnitude, depending on current flow and lunar phase, from a minimum of 23 km and 12 km in *H. spinosissimus* and *H. comes* respectively, to a maximum of 211 km for both species (Table 4).

DISCUSSION

Tropical seahorses, like most reef fishes, have a pelagic phase in which at least some portion of paternally-brooded young disperse planktonically. Densities of *Hippocampus spinosissimus* were approximately five times more abundant than *H. comes*, which may represent real differences in the population sizes of these niche-separated congeners. *Hippocampus spinosissimus* and *H. comes* have pelagic phases inferred to last between 5-10 days. This is among the shortest planktonic periods reported in small demersal reef fishes, which normally disperse over 20-30 days. Shorter planktonic periods are common to invertebrate larvae (e.g. 8-10 days), which, like seahorses, have poor swimming abilities relative to perciform reef fishes. Indirectly, we estimated that *H. comes* and *H. spinosissimus* may disperse on the order of 20-200 km from natal reefs, depending on tidal cycle, currents and bathymetry. Variation in tidal flows due to lunar phase is particularly relevant to species such as seahorses that have short dispersal windows, or spawning that is timed to coincide with particular tides (Robertson et al. 1990).

Planktonic Phase

Reef fishes without a planktonic phase are rare, but do exist in the families Apogonidae, Batrachoididae, Bythitidae, Pholidichyidae, Plotosidae, Pomacentridae, and Sciaenidae (Leis 1991; Leis & McCormick 2002). Until recently, there had been debate whether, because of their extreme form of brooding parental care, the developed nature of young at birth and the morphology of young apparently unsuited to a planktonic existence, seahorses might lack a planktonic phase. The presence of tropical seahorse young in the plankton indicate that bipartite reef fish life histories persist in marine taxa with morphological and behavioural traits apparently ill-suited to a planktonic phase or enabling immediate settlement (e.g. heavy pigmentation, young metamorphosed upon release, and the ability to grasp structure with prehensile tails within hours after release).

This study, as well as recent literature, now confirm that many seahorses, and perhaps the genus *Hippocampus*, share a bipartite life history with most marine fishes and invertebrates (Strathmann 1990). Our work and at least three other publications (Kanou & Kohno 2001; Perez-Ruzafa et al. 2004; Vandendriessche et al. 2005) confirm a planktonic phase in five seahorse species (Table 5). Anecdotal accounts from aquarium facilities and field observations also provide evidence for pelagic behaviour in small young of a further seven seahorse species including; *H. bargibanti, H. breviceps, H. capensis, H. hippocampus, H. kuda, H. reidi, H. subelongatus* (Foster & Vincent 2004a) . These species range in size from among the smallest (e.g. *H. bargibanti*) to the largest (*H. abdominalis*) of the genus, and inhabit coasts from the equator to temperate latitudes. *Hippocampus fuscus* is the only seahorse species reported to settle immediately after release, but under aquarium conditions (Golani & Fine 2002).

Abundance

Planktonic seahorse densities in this study and elsewhere are universally low (Table 5) and what variation does exist may be related to coastal productivity or the topography of coastlines. In general, records of seahorses from ichthyoplankton surveys are uncommon. This is likely because densities are naturally low and hence difficult to work with in the context of formal hypothesis testing. In this study, densities and tow occupancy of *H. spinosissimus* and *H. comes* were lower than *H. mohnikei* in Tokyo Bay, but generally comparable to *H. abdominalis* studied in New Zealand (Table 5). Compared with continuous coastlines (e.g. New Zealand) and oligotrophic archipelago systems (e.g. Danajon Bank, Philippines), unusually high densities of planktonic young have been found in enclosed bays and coastal lagoons, where flushing is constrained and where biological productivity is the highest among marine habitats (Allongi 1998). For example, in the Mar Menor, Spain, 100 % of tows captured *H. guttulatus* (Perez-Ruzafa et al. 2004). A comparable lagoon on the Portugal coast has areas where densities of adult *H. guttulatus* are 1-3 orders of magnitude greater than observed in the Danajon Bank and other, unfished seahorse populations (Curtis & Vincent 2006; Foster & Vincent 2004a; Morgan & Vincent 2007).

The large difference in planktonic abundance of *H. spinosissimus* versus *H. comes*, may reflect relative differences in the abundance of these two species in the Danajon Bank. In this region, densities of *H. comes* are well-documented from fisheries-independent surveys (Marcus et al. 2007; Morgan & Vincent 2007), while densities of *H. spinosissimus* remain unstudied. However, catch per unit effort data from both species indicated that breath-hold divers caught an average of only 2 ± 5 (SD) *H. comes* per night (Project Seahorse, unpublished data). In contrast, compressor divers moving at comparable swimming speeds and able to search a similar area, caught an average of 25 *H. spinosissimus* at the advent of a recent deep-water fishery (Panes & Giles 2004). These differences in adult abundance between *H. spinosissimus* and *H. comes* are broadly comparable with the interspecific differences observed in the density of young from plankton tows. These differences support the possibility that *H. spinosissimus* in the Danajon Bank could have a substantially larger effective population size than *H. comes.* Sandy-silt bottoms, occupied by *H. spinosissimus* (Morgan & Panes 2007), are common throughout most of the Danajon bank and comprise substantially more area than shallow algal and reef environments used by *H. comes* (Perante et al. 2002; Pichon 1977).

The most parsimonious explanation for observed size and depth distributions of *H. spinosissimus,* is that seahorses release their broods at night, as noted in *H. whitei* (Vincent 1995). Consistent with nocturnal births, lengths of individuals in night tows corresponded well to size at release (6-7 mm) (Lourie et al. 2004) and densities were higher than in day tows. Overall densities should be highest soon after birth, when fewer young will have perished or been preyed upon. High natural mortality is the norm for marine larvae, where rates (m) for young in the plankton are commonly >0.1 d^{-1} (estimated as $N_t = N_o e^{-mt}$) (Hewitt 1985; Houde 1994; Rumrill 1990; Strathmann 1985, 2007). Tows with greatest densities also captured the smallest individuals. This may be because immediately after release, members of broods would still be found physically close together in the water column. Similarly and perhaps not exclusively, small, newly released young may also be concentrated in surface waters because they are not yet competent to regulate their buoyancy. Observations from tows and aquarium rearing confirm that immediately after birth, juvenile seahorses rise quickly to the surface (Chapter 1). As visual ambush feeders (Foster & Vincent 2004a; James & Heck 1994), it is unlikely that seahorse young migrate vertically to follow prey to the surface at night. The limited swimming abilities of seahorses, certainly early in the pelagic phase (Chapter 1) and even as adults (Blake 1976), also makes it unlikely that diel differences in net avoidance (e.g.

Brander & Thompson 1989; Overton & Rulifson 2007) accounted for observed difference in density.

Rafting

Our findings do not support the proposal that rafting is a dispersal mechanism commonly used by seahorses during their planktonic phase, nor do they conclusively refute this possibility. In tows, we regularly observed small juvenile pipehorses (also family Syngnathidae) that were rafting and attached to plant fragments at capture. In contrast, no seahorses were found grasping organic debris in tows, and the abundance of seahorse young showed no relationship with the availability (mass) of floating debris. In our study area, narrow diameter organic debris (*Syringodium sp*.) was available in most tows, and we observed that seahorse young will grasp these fragments (Chapter 1). It remains possible that seahorses may have been captured while rafting, but detached during towing. Low seahorse densities may have also precluded the ability to detect a predictive relationship between seahorse abundance and floating debris. Furthermore, some debris may not be useful for rafting by small seahorses: future research might consider partitioning debris by diameter and testing these relationships against seahorse abundance.

Our results do not preclude the possibility that rafting may still mediate rare long distance dispersal events, which could occur during the planktonic phase and/or under unusual circumstances (e.g. during typhoons) and/or at larger life stages. In temperate areas, both pipefishes and *H. abdominalis* have been found in association with drift algae (Kingsford 1992; Kingsford & Choat 1985). Compared with regular, but infrequently successful recruitment by pelagic propagules, the movement of even a small number of reproductive adults can have important and demographic and genetic consequences including successful founder events and range extensions (Johannesson 1988).

Planktonic Duration and Dispersal Distance

The estimated planktonic periods of *H. comes* and *H. spinosissimus* are short compared with other reef fish species, and are more comparable to a suite of invertebrates that exhibit planktonic durations of ca.10 days (summarized in Bonhomme & Planes 2000, but see longer periods for decapods in Sale & Kritzer, 2003). Differences in the pelagic duration of reef fishes versus invertebrates may arise from disparities between the swimming abilities in these two groups. Extended dispersal distances are more likely to evolve in species with the ability to locate and move back to suitable settlement habitat (Dytham 2003). In this situation, there are few costs but apparent benefits to moving away from reefs and associated predation during the larval period (Hoey & McCormick 2004; Johannes 1978). Such movement is within the capabilities of many larval reef fishes, which exhibit remarkable swimming and sensory ability prior to settlement, allowing them to orient and swim long distances over extended periods (Leis & McCormick 2002). Larval fish have significantly faster swimming speeds than larval invertebrates and relatively fewer invertebrate taxa have evolved effective swimming abilities (Bradbury & Snelgrove 2001). Most invertebrate species that do swim, use cilia and/or muscular contraction against a rigid skeleton or translate vertically in the water column (Chia et al. 1984). At least early in their pelagic phase, seahorse young move passively with ambient currents (Chapter 1) and even as adults, seahorses possess limited swimming ability via weak dorsal fin propulsion (Blake 1980). Weak swimming is consistent with selection favouring the relatively shorter pelagic duration seen in seahorses.

Modelling has shown that the arrangement of habitat in space and its distribution in time (susceptibility to disturbance) may have profound effects on the evolution of dispersal (Dytham 2003; Travis & Dytham 1999). For higher density habitats, there is a greater likelihood of dispersal away from natal patches, because the chance of returning to suitable habitat during the competency period is higher (Travis & Dytham 1999). This suggests that deep-water groups that inhabit the matrix surrounding patchy shallow habitat should disperse more readily than shallow-water species. The apparently reduced planktonic duration (shorter minimum dispersal period) observed in the shallow-dwelling *H. comes* versus the deep-water dwelling *H. spinosissimus* (with a maximum dispersal period that may exceed conservative estimates here), is consistent with this theory. Lourie et al. (2005) also noted potential relationships between habitat use and dispersal capacity (inferred genetically) among seahorses. Greatest dispersal capabilities, indicated by widespread haplotypes, belonged to a deep-water species (*H. trimaculatus)* while the least widespread haplotypes were seen in a shallow, seagrass-dwelling species (*H. barbouri*) (Lourie et al. 2005). *Hippocampus spinosissimus*, like *H. trimaculatus*, associates with structure on expansive, sandy or silty-bottoms, at depths ranging from 8-70+ m (Morgan & Panes 2007). In contrast, *H. comes,* like *H. barbouri,* is a shallow-dwelling species that occupies macroalgal beds and coral reefs (<10 m deep) found in narrow bands encircling islands (Morgan & Vincent 2007). Similarly, in the Red Sea endemism is higher among species in shallow waters than it is among deep-water groups (Goren 1986). One of the only other reef fish with a pelagic phase comparable to seahorses (9-12 days) is the Panda Clownfish, *Amphiprion polymnus*, which also exhibits obligate associations with rare, large anemones, often spaced at distances >10 km (Jones et al. 2005; Thresher et al. 1989).

We acknowledge two considerations that may have influenced our estimates of planktonic duration for seahorses. First, growth rates used to infer planktonic duration from the size of individuals in tows may have been affected by aquarium-rearing, either upwards or downwards relative to in situ growth. Furthermore, if growth varies throughout the planktonic phase, size may not clearly reflect age/planktonic duration. However, for species such as gobies and pomacentrids, size at settlement is known to reflect the length of planktonic life (Sponagule & Cowen 1994; Wellington & Victor 1989). Most species that are able to reduce growth prior to settlement, tend to do so by delaying metamorphosis (Victor 1986). This is not possible for seahorses, which develop directly. Second, logistics dictated that drifters in this study be deployed prior to ichthyoplankton surveys, but all occurred during the September to January period of the Philippines "dry" northeast monsoon (Green et al. 2000). Our estimated dispersal distances may therefore under-represent transport during the height of the northeast monsoon from November to January and over-represent transport during the calm February to May inter-monsoon window. A second "wet" south-west monsoon period also begins in late June (Wang & Ho 2002).

Dispersal distances observed here are in keeping with observations from other coral reef fishes, which are now believed to move on the order of 10s to 100s of km (Cowen et al. 2006). These scales of connectivity mean that in reefs and archipelagos, patch populations should receive meaningful demographic support from neighbouring upstream patches, as well as occasional long distance dispersers that will influence genetic diversity (but not population dynamics), from patches further afield (Mora & Sale 2002). Dispersal distance inferred here, support assertions by Lourie (2004) from genetic research, that extirpated populations of seahorses, separated by hundreds of kilometers, may not be quickly recolonised. Therefore, heavy fishing has the potential to cause lasting local depletions and fishing grounds may need to recover without meaningful input of recruits from elsewhere. This study also provides first indications that seahorses should be able to move between and perhaps among, the network of small marine protected areas in the Danajon Bank, spaced at intervals of <10 km. Similarly, fishing pressure exerted by upstream communities will impact the catch of neighbouring downstream municipalities. The scale of these effects presents the incentive for fishers to collectively manage their shared resources on a regional scale.

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Table 1. Summary information for seahorses caught in n = 244 plankton tows from November 2002 to January 2003 in the Danajon Bank, Philippines. SLc = curved standard length, SE = standard error.

Species	**n**	**Density (ind. X 1000 m^{-3})**	**Density SE (ind. X 1000 m^{-3})**	**Mean SLc (mm)**	**SLc SE (mm)**	**SLc_{min} (mm)**	**SLc_{max} (mm)**
H. spinosissimus	73	0.51	0.16	10.07	0.31	6.40	23.65
H. comes	11	0.09	0.14	13.59	0.66	9.53	16.78
Total	84	0.60	0.09	10.53	0.31	6.40	23.65

Table 2. Summary statistics from two-way analyses of variance used to test the effects of time of day and depth on seahorse abundance and size from 244 ichthyoplankton tows from November 2002 to January 2003 in the Danajon Bank, Philippines. df = degrees of freedom. ANOVA was tested at $\alpha = 0.05$, where NS indicates the absence of a significant result ($p>0.1$), ~ indicates $0.05<p<0.1$, and * indicates the presence of a significant result ($p<0.05$).

Model	Source of variation	df	F	*p*	
	***H. spinosissimus* (n = 73)**				
Density	Overall model	3	2.24	0.084	~
	Time	1	3.71	0.055	~
	Depth	1	2.11	0.147	NS
	Time*Depth	1	0.73	0.394	NS
Size	Overall model	3	4.15	0.009	*
	Time	1	0.89	0.350	NS
	Depth	1	7.50	0.008	*
	Time*Depth	1	0.31	0.578	NS
	***H. comes* (n = 11)**				
Density	Overall model	3	1.34	0.260	NS
	Time	1	0.00	0.960	NS
	Depth	1	4.02	0.046	*
	Time*Depth	1	0.00	0.992	NS
Size	Overall model	3	0.58	0.646	NS
	Time	1	0.63	0.454	NS
	Depth	1	0.73	0.422	NS
	Time*Depth	1	0.01	0.948	NS

Table 3. Spearman rank correlations, tested at $\alpha = 0.05$, for relationships between biomass of floating debris (g) and seahorse density (*H. spinosissimus* m^{-3} and *H. comes* m^{-3}) for all tows, and only those tows capturing young. Mean debris values (g) are followed by minimum and maximum masses of dried debris captured tow^{-1}. SE = standard error, df = degrees of freedom, r_s = Spearman rank correlation coefficient. For samples <10, r_s values were tested against tables of critical values to evaluate p values, and otherwise, were calculated as per Sokal & Rohlf (1995).

Analysis	Correlate	Mean debris ± SE	df	r_s	*p*
			H. spinosissimus		
All tows	Total debris	7.94 ± 2.2 (0-434.7)	2,225	0.034	0.61
	Organic debris	7.85 ± 2.2 (0-432.9)	2,225	0.039	0.56
Tows with seahorses	Total debris	4.38 ± 1.7 (0-59.7)	2,42	0.138	0.37
	Organic debris	4.15 ± 1.5 (0-50.5)	2,42	0.108	0.49
			H. comes		
All tows	Total debris	7.94 ± 2.2 (0-434.7)	2,225	0.098	0.14
	Organic debris	7.85 ± 2.2 (0-432.9)	2,225	0.098	0.14
Tows with seahorses	Total debris	2.08 ± 1.2 (0.02-11.5)	2,8	0.321	>0.1
	Organic debris	2.08 ± 1.2 (0.02-11.5)	2,8	0.321	>0.1

Table 4. Range of estimated dispersal distances for *H. spinosissimus* and *H. comes* based on size and associated pelagic duration (PD), lunar phase and flow patterns, in the Danajon Bank. Size is measured as curved standard length (mm).

Species	**Dispersal distances**	**Size of sampled individual (mm)**	**PD (days)**	**Period of lunar cycle**	**Current**	**Mean Current speed (km hr^{-1})**	**Estimated dispersal distance (km)**
H. spinosissimus	Upper maximum	Smallest settled, 26.7	10.4	Spring tide	Unidirectional	0.87	211
	Lower maximum	Smallest settled, 26.7	10.4	Neap tide	Net	0.15	35
	Upper minimum	Largest planktonic, 23.6	8.7	Spring tide	Unidirectional	0.92	193
	Lower minimum	Largest planktonic, 23.6	8.7	Neap tide	Net	0.14	23
H. comes	Upper maximum	Smallest settled, 26.7	10.4	Spring tide	Unidirectional	0.87	211
	Lower maximum	Smallest settled, 26.7	10.4	Neap tide	Net	0.15	35
	Upper minimum	Largest planktonic, 16.8	4.9	Spring tide	Unidirectional	0.92	88
	Lower minimum	Largest planktonic, 16.8	4.9	Neap tide	Net	0.14	12

Table 5. Summary table of studies with quantitative information for *Hippocampus* spp. found in the plankton. “Seahorses” gives the total number of animals found among tows “With Seahorses”, from some total number of “Tows”. Planktonic size is given as a range, where available, with the measurement method in brackets, where SLc = curved standard length, SLs = straight standard length, Ht = Height (sensu Lourie 2003), TL = total length (sensu Kanou & Kohno 2002), and NN = not noted. Planktonic densities are recorded in mean individuals per 1000 m^3 of water ± SE. % Occ. gives the percentage of tows containing young from the total number of tows.

Species	Study type	Study Date	Seahorses	With seahorses	Tows	Tow depth	Planktonic size range (mm)	Planktonic density	% Occ	Reference
abdominalis Kaikoura coastline, New Zealand	neuston transects at distances 0.5, 2, 4, 6 km from shore	Oct. 1995–May 1997	28	23	444	surface	12.5-73.0 (SLs)	0.13 +/- 0.03	5.2	Hickford & Schiel 2003 M.Hickford, unpublished data
abdominalis Kaikoura coastline, New Zealand	neuston & oblique transects 0.5 km from shore	Oct. 1995–May 1997	(0 m): 48 (1 m): 53 (3 m): 4	38	216	surface, 1 m, 3 m	(0 m): 10.9-97.7 (1 m): 10.6-16.8 (3 m) 13.5– 13.9 (SLs)	0.97 +/- 0.21	17.6	M.Hickford, unpublished data
abdominalis North Island, New Zealand	seines set around drift algae and neuston tows	1981-1982	NN	NN	NN	surface, seine	“Adult”	NN	NN	Kingsford & Choat 1985
comes Bohol Province, Philippines	neuston and oblique transects at variable depths and distances from shore	Nov. 2002-Jan. 2003	11	10	244	surface, 5 m	9.5-16.8 (SLc)	0.09 +/- 0.03	4.1	This study
guttulatus Mar Menor, Spain	neuston transects at variable distances from shore	Feb 1997–Dec. 1997	245	NN	NN	0.5-2 m	7.6-33.8 (NN)	3.7 +/- 0.04	100	Perez-Ruzafa et al. 2004
guttulatus French-Belgian border	neuston transects	Aug. 2003	2	1	6	surface	29.3, 35.1 (Ht)	NN	NN	Vandendriessche et al. 2005
mohnikei Tokyo Bay, Japan	neuston & oblique transects, at variable depths and distances from shore	Aug. 1995–Dec. 1999	206	NN	218	surface, 0-10m	6.0-65.3 (SLs)	0.94 (ind* tow^{-1})	NN	Kanou & Kohno 2001
spinosissimus Bohol Province, Philippines	neuston & oblique transects at variable depths and distances from shore	Nov. 2002-Jan. 2003	72	46	244	surface, 5m	6.4-23.6 (SLc)	0.51 +/- .09	18.9	This study

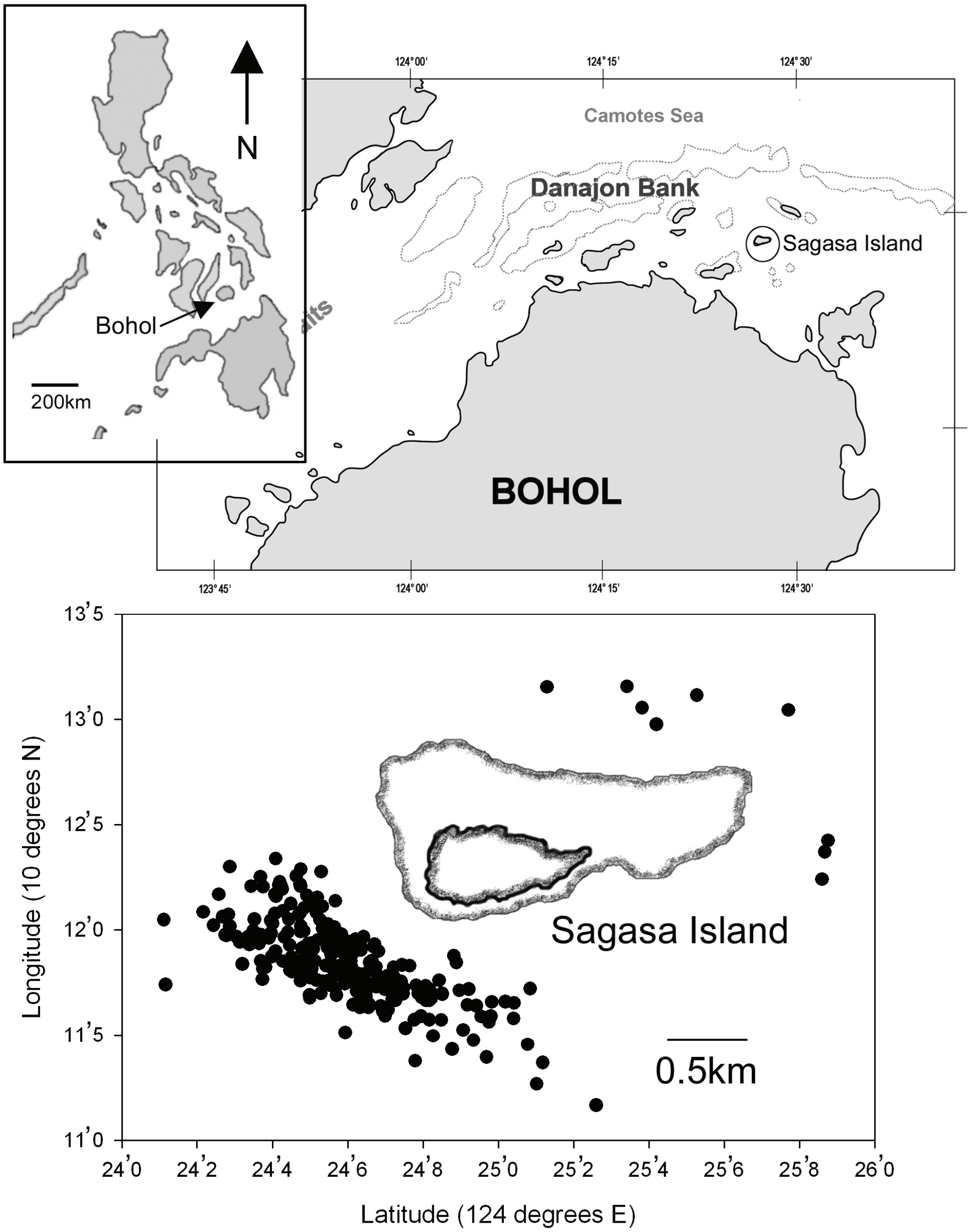

Figure 1. Location of study site at Sagasa Island (10°12.05'N, 124°.75'E), in the Danajon Bank, north coast of Bohol province, Philippines. Black points in the lower figure represent the location of ichthyoplankton tows (n = 244) conducted in community-sanctioned areas around Sagasa Island.

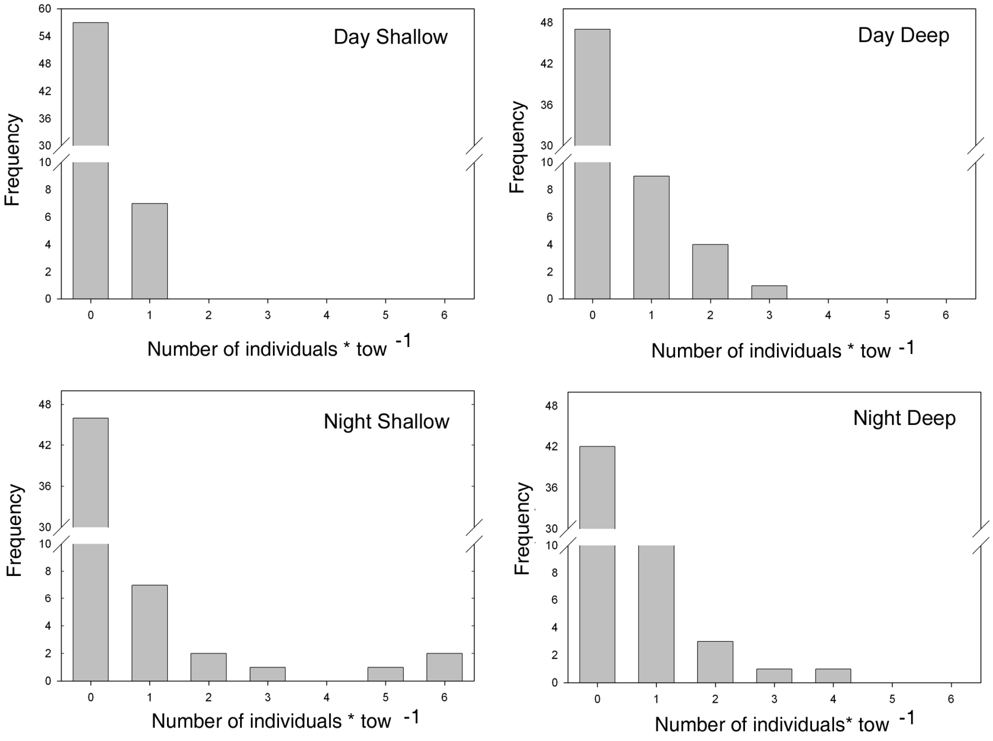

Figure 2. Frequency distributions of seahorses caught per tow, stratified by time of day and depth. Note breaks on ordinate axes. Shallow neuston tows were at the surface and deep oblique tows were at 5 m depth.

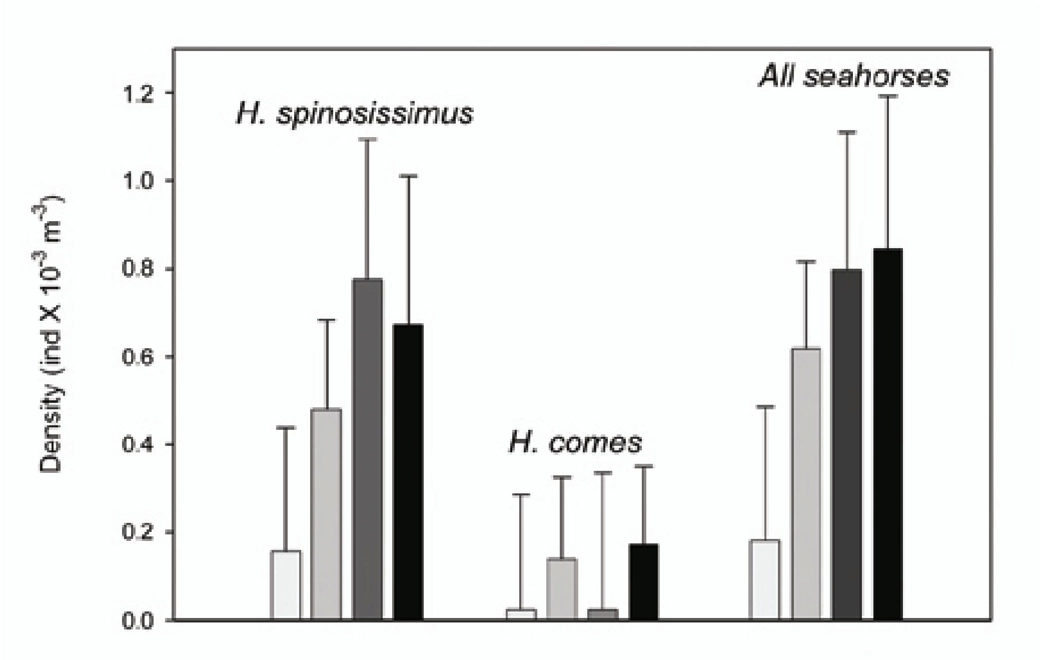

Figure 3. Mean densities of seahorse young caught in n = 244 ichthyoplankton tows at Sagasa Island, central Philippines. Time of day and depth of tow are indicated by bar colour: white □ = shallow (neuston) day tows; light gray ▒ = deep (oblique) day tows; dark gray ▓ = shallow (neuston) night tows; black = deep (oblique) night tows. Error bars give the standard error of the mean.

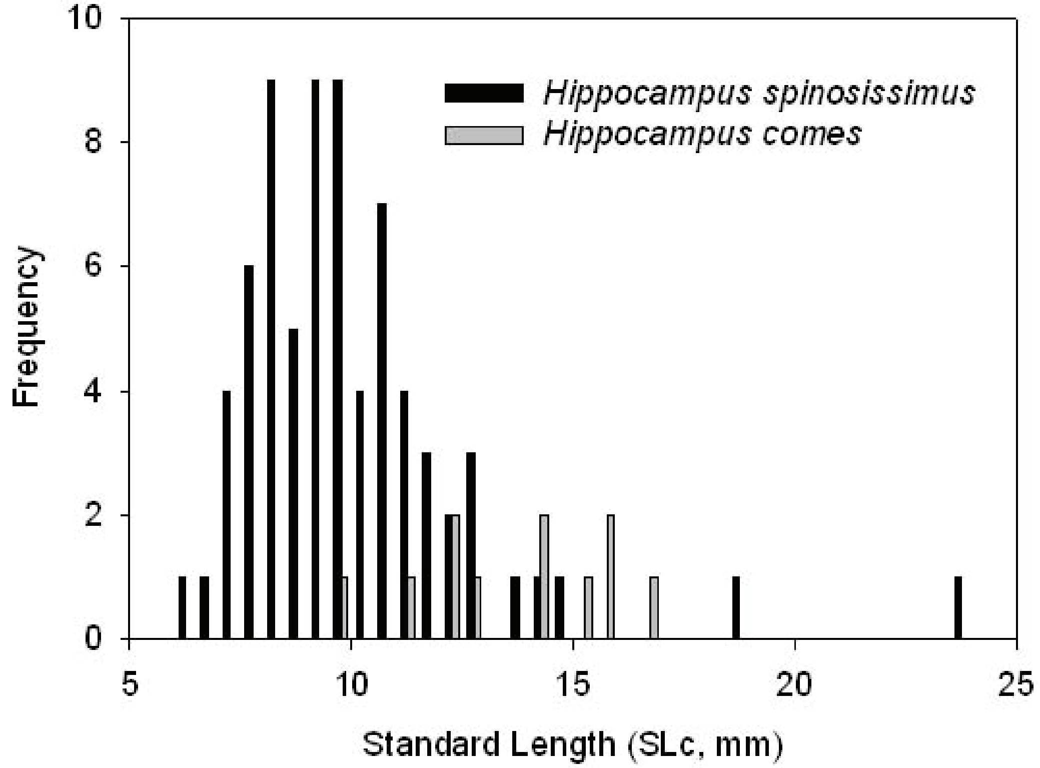

Figure 4. Size frequency distributions of *H. spinosissimus* (n = 73) and *H. comes* (n = 11) young taken in ichthyoplankton tows (n = 244) near Sagasa Island in the Danajon Bank, central Philippines.

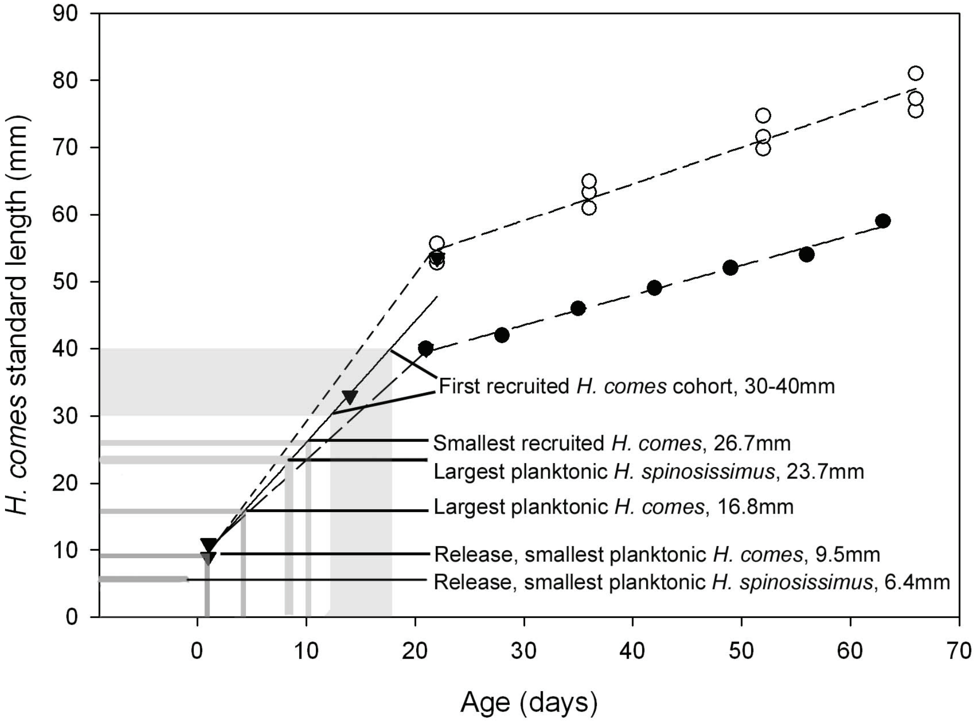

Figure 5. Growth of *H. comes* reared ex situ over the first 66 days after release. Gray shading shows (vertically) the sizes and (horizontally) day ages of biologically meaningful individuals from tows, described in Table 4. Black points (means from n = 10 individuals in a single tank) show values from Job et al. (2006) and white points (means from n = 15 individuals, among 3 replicate tanks at each age) are unpublished data collected by K. S. Truong. For husbandry methods, see Appendix I. Black triangles are intermediate values calculated from the two illustrated growth trajectories using information only up to 21 days and fitted by least squares regression.

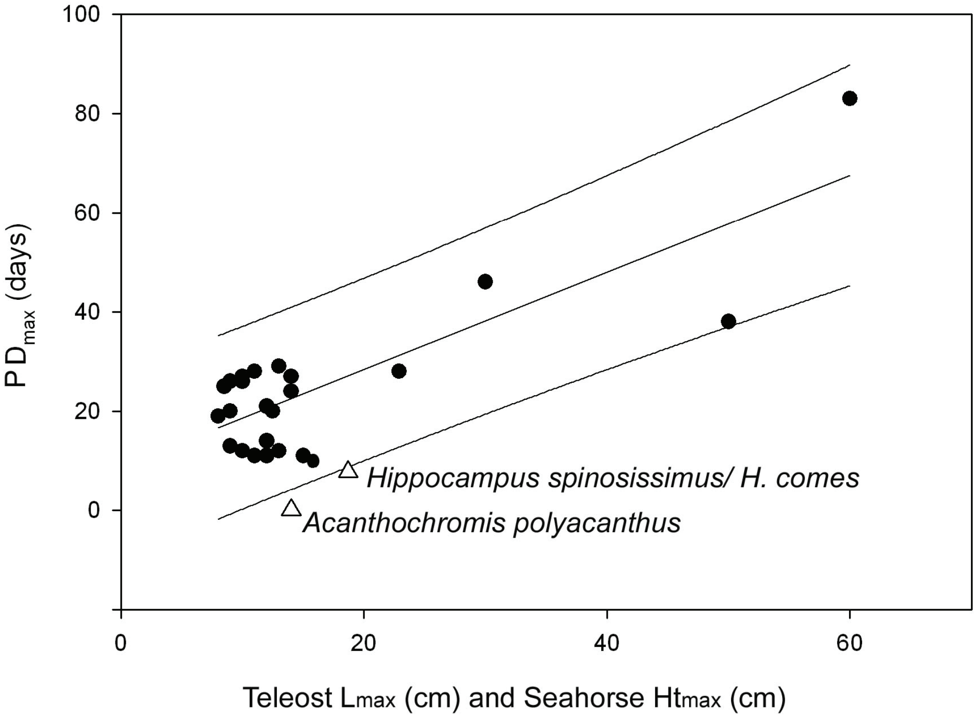

Figure 6. Spearman rank correlation ($r_s = 0.43$) between maximum length and maximum pelagic duration (PD_{max}, days) for fish species that guard/bear live young, from tropical waters ($n = 24$). Maximum length is given as standard length (L_{max}, cm) for teleosts and as maximum height (Ht_{max}, cm) for seahorses. Upper and lower lines represent 95 % prediction intervals. Data were taken from Fish Base, http://www.fishbase.org, and from Bonhomme & Planes (2000), Appendix A.

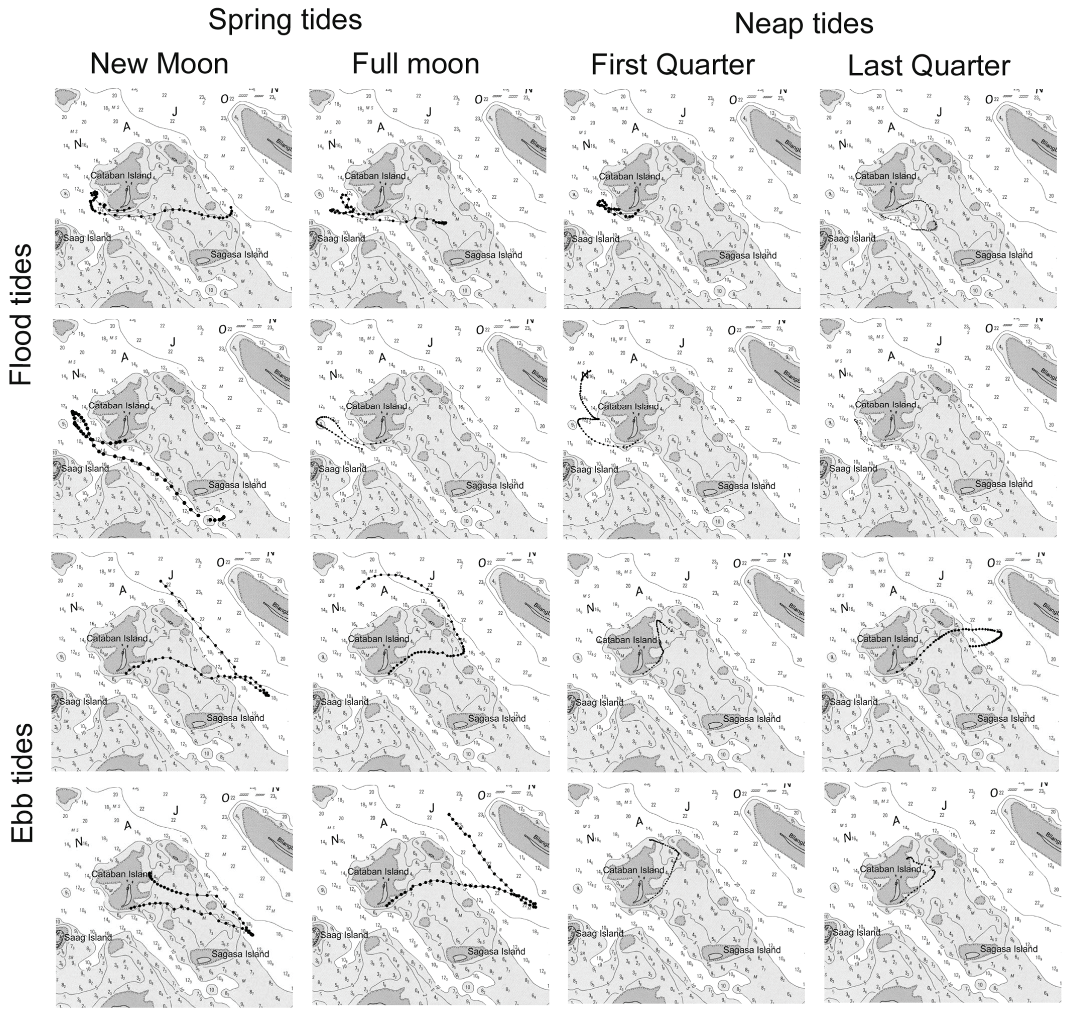

Figure 7. Drifter tracks indicate total and net distances traveled over one full tidal cycle (Flood = flood tide followed by ebb tide, Ebb = ebb tide followed by flood tide) for both spring and neap tides using a surface Lagrangian drifter, from October to November of 2002. All tracks start at the dark area demarcating the reef flat of Cataban Island, Bohol, Philippines. Points on tracks indicate GPS coordinates recorded every 15 minutes.

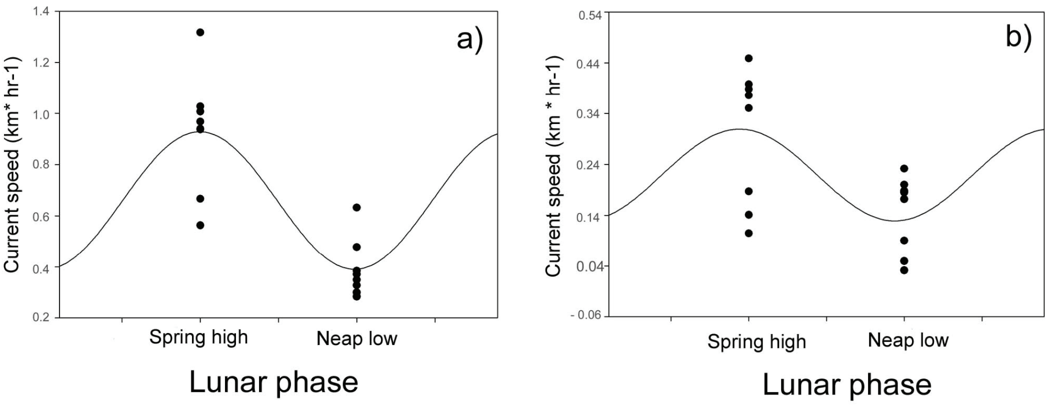

Figure 8. Spring and neap current speeds when presuming: a) unidirectional and b) net flow. Unidirectional flow corresponds to currents speeds inferred from total distances traveled by drifters per unit time. Net flow corresponds to current speeds inferred from distances traveled between the start and end point of drifters per unit time.

Appendix I – Husbandry Methods For Captive-reared *H. comes*

***Hippocampus comes*, Curve 1, open circles, Figure 5. (Dr. S. K. Truong, pers. comm.)**

Young were reared from a single *H. comes* father at the Nha Trang Institute of Oceanography on one bio-filtered saltwater system. Animals were reared in triplicate 120 L aquariums with 300 % water changes each day. From 1-35 days of age, young were reared in 2 m^3 composite tanks and were fed live copepods (saturate) maintained at a density of 10-20 copepods mL^{-1}. From the age of 35 days post-hatch, seahorses were weaned onto mysis shrimp, fed 3 times daily until satiation. Temperature, pH, and ammonia levels were monitored 3 times per month throughout the culturing period. Temperature values ranged between 26-30° C, pH between 8-8.2 and ammonia was maintained at <1 mg L^{-1}.

***Hippocampus comes*, Curve 2, closed circles, Figure 5. (reproduced from Job et al. 2006).**

H. comes were cultured at the Institute of Oceanography in Nha Trang (Vietnam) as part of a joint seahorse conservation project between Project Seahorse (http://www.projectseahorse.org) and the Institute of Oceanography (Vietnam). Four hundred and thirty newly-hatched *H. comes* from a single batch were reared for a period of 63 days (9 weeks). From hatching until the age of 27 days, the young seahorses were reared in a single 3.5 m^3 circular nursery tank. The young seahorses were fed with wild-caught zooplankton (approximately 80 % copepods) for the first 10 days. The zooplankton was collected using a 210 µm net. From the age of 7 days post-hatch, the seahorses were weaned onto 2 day old brine shrimp, which remained their sole diet until the age of 27 days. Prey density was maintained at 1-2 individuals mL^{-1} in the nursery tank.

On the 28th day after hatching, the seahorses were counted, and then split into three equally-sized groups and reared for a further 5 weeks in three separate 3.5 m^3 circular grow-out tanks. Seahorses in the grow-out tanks were fed with 3-4 day old brine shrimp from the age of 28 days to the end of the grow-out period at 63 days of age. Prey density was maintained at 0.1-0.2 individuals mL^{-1} in the grow-out tanks. Five seahorses were sampled from each of the three grow-out tanks at weekly intervals starting from the age of 28 days, and their standard length and height measured. All seahorses were counted at the end of the 63 days. In both the nursery tank and the grow-out tanks, sampled seahorses were placed in a separate tank after measurement so as not to recount them in following weeks.

Brine shrimp used to feed the seahorses were fed with *Chaetoceros sp.* diatoms. The brine shrimp were enriched with blended *Acetes sp.* for an hour prior to being fed to the seahorses (cf. Job et al. 2002). *Acetes sp.* is a planktonic crustacean abundant throughout Southeast Asia. The enrichment product was obtained by blending *Acetes sp.* paste and sieving it through a 53 µm sieve. Only the filtrate was used to enrich the brine shrimp. The seahorses were fed twice a day. The nursery and grow-out tanks were linked to a 60 000 L recirculating seawater system. Temperature, salinity, pH, ammonia, nitrite and nitrate levels were measured biweekly in the seawater system throughout the culturing period. Temperature, salinity and pH values were 29 ± 0.45° C, 31.15 ± 0.21 ppt, and 8.25 ± 0.05 respectively. Ammonia, nitrite and nitrate concentrations were all less than 0.1 mg L^{-1}. The flushing rate through the nursery and grow-out tanks was 20 L min^{-1}. A strainer over the overflow ensured that no seahorses or food items were flushed out of the tank.

LINKING STATEMENT III

In Chapters 1 and 2, I investigated where tropical seahorses are in space and how they use their environment during the earliest part of their life history. In Chapter 1, I described how seahorse young behave early in the dispersive phase, within days after birth and in Chapter 2, I showed where young are in the water column and how far they may move from natal reefs. These results contradicted some expectations that seahorses, with their unusual morphology and advanced development at release, would not disperse as readily as other teleosts. Instead, findings indicate that tropical seahorses have a short planktonic phase, but do exhibit a bipartite life history, consistent with most other coral reef fish families.

Like newborns, little was known about the ecology of settled juveniles after recruitment from the water column to the benthos. Therefore, I sought to locate rearing grounds and to understand how associations between *H. comes* and benthic structure shift with age at the scale of communities (e.g. coral reef, wild macoroalgal beds) and holdfasts (e.g. coral heads, algal thalli). In tropical reef systems, research on habitat association tends to focus dichotomously on seagrass/mangrove nurseries and reef-associated adults. In this chapter I exerted considerable effort to examine associations with (both wild and farmed) macroalgal beds which are important zones in this and other reef systems. Understanding the spatial distribution of structured populations has important implications for understanding species' ecology and how fitness trade-offs change with size. These data will make it possible to build habitat suitability models and to target appropriate locations for future research or spatial management, relevant to specific life stages.

CHAPTER 3

THE ONTOGENY OF HABITAT ASSOCIATIONS IN THE TROPICAL TIGER TAIL SEAHORSE *Hippocampus comes* Cantor, 1850.

ABSTRACT

This study examined how habitat associations changed with ontogeny in the tiger tail seahorse *Hippocampus comes* Cantor 1850, over four reef zones in a coral reef ecosystem. *Hippocampus comes* showed ontogenetic differences in their use of habitat at the scale of reef zones (macrohabitat) and holdfasts (microhabitat). Across reef zones, juvenile size classes (25-105 mm standard length (curved), SLc) were most abundant in wild macroalgal beds (*Sargassum* spp.) (55.7 %), while adults (>105 mm SLc) occupied both coral reefs (39.7 %) and macroalgal beds (42.7 %). Microhabitat use also varied with ontogeny. Juveniles generally used macroalgal holdfasts, while adults >135 mm SLc used a greater diversity of specialized microhabitats that included branching sponges, branching corals and tall seagrass. Ontogenetic changes in habitat association, as well as size-related shifts in crypsis and aggregation, suggest that *H. comes* experiences fitness trade-offs that vary with size; juveniles may associate with habitat that reduces predation, while larger individuals may use distinct microhabitat in reef zones to optimize reproductive success. Results are discussed in the context of targeted exploitation, expanding artisanal mariculture, habitat damage from illegal fishing and reserve design.

INTRODUCTION

Ontogenetic shifts in habitat use commonly arise from changing resource needs as organisms grow. The size of individuals within species often spans at least one order of magnitude, and may differ by four orders of magnitude or more in fishes (Werner & Gilliam 1984). The ability of species to partition resources, including habitat, should be favoured by natural selection, conferring greater fitness to species that avoid direct competition with conspecifics. In fishes, changes in habitat occupancy may provide: (1) refugia to avoid predation (Beukers & Jones 1997; Foster et al. 1988; Hixon & Beets 1993), (2) shelter from abiotic conditions (Steele 1999), (3) opportunities to obtain prey items (Cocheret de la Morinière et al. 2003a; Cocheret de la Morinière et al. 2003b), (4) access to mates (Alonzo 2002), or more than one of the above. Trade-offs among shifting needs will drive fishes to use different habitats at different sizes, with either gradual or rapid transitions (McCormick & Makey 1997; Werner & Gilliam 1984).

Reef fish life histories, and hence habitat use, have traditionally been considered bipartite; young occupy open ocean during initial dispersal then move to the benthos as sedentary adults (Barlow 1981; Leis 1991; Leis & McCormick 2002). These life histories, however, also include a third, sometimes ephemeral intermediate phase when juveniles settle and exhibit ecology distinct from both planktonic larvae and settled adults (Lecchini & Galzin 2005). This period and the ensuing shift to adult habitat have been investigated at various spatial and temporal scales from reef fish families that include Apogonidae (Vagelli 2004), Haemulidae (Cocheret de la Morinière et al. 2003b), Labridae (Green 1996), Lutjandidae (Cocheret de la Morinière et al. 2003b), Mullidae (Meyer et al. 2000), Pomacentridae (Lirman 1994) and Serranidae (Dahlgren & Eggleston 2001; Eggleston 1995; Light & Jones 1997).

Research on habitat use by juvenile reef fishes has generally lagged behind that on adults. Young can be difficult to monitor because of size, mobility, crypsis and variability in the timing and magnitude of recruitment events (Doherty & Williams 1988). In addition, small fishes can be challenging to tag (Beukers et al. 1995; Olsen & Vøllestad 2001) and are subject to high mortality (Carr & Hixon 1995; Hoey & McCormick 2004; Searcy & Sponagule 2001). Research on juveniles has therefore focused generally on species that are reef-associated and relatively simple to census [e.g. damselfishes, (Bay et al. 2001)], or of commercial importance [e.g. coral trout, *Plectropomus leopardus* (Lacepède, 1802) (Light & Jones 1997); Nassau grouper *Epinephelus striatus* (Bloch, 1792) (Dahlgren & Eggleston 2001); gag, *Mycteroperca microlepis* (Goode & Bean, 1880) (Ross & Moser 1995)].

Only recently have various habitats been investigated for the role they play as rearing grounds for coral reef fishes, and usually only at the scale of communities. Seagrass meadows and mangrove forests have often been documented as areas occupied by a variety of juvenile demersal and pelagic tropical fish species (Mumby et al. 2004; Nagelkerken et al. 2001; Nagelkerken et al. 2002; Nagelkerken et al. 2000). Juvenile reef fishes also show less documented associations with back reefs, lagoon patch reefs and rubble fields (Adams & Ebersole 2002). It is unclear whether, or how, juvenile tropical reef fishes associate with microhabitat used by young in temperate zones, such as oyster and cobble reefs (Heck et al. 2003), algal turf, sea urchins and boulders (Gonçalves et al. 2002). A recent review of seagrass and associated nursery literature indicated that the general presence of three-dimensional structure may be more important than the type of structure per se, in determining a habitat's nursery value (Heck et al. 2003).

As with juveniles, adult reef fishes show strong habitat associations, coupled with behaviours that include site fidelity and low net movement (Sale 1978). Even more closely associated with the reef matrix are cryptobenthic reef fishes, which show tight, often obligate relationships with their immediate surroundings (Depczynski & Bellwood 2004). Seahorses are an example of a cryptobenthic reef fish genus (*Hippocampus* spp.) that are usually well hidden, and as adults, exhibit high site fidelity, small home ranges and limited swimming ability compared with most teleosts (Foster & Vincent 2004a; Perante et al. 1998). Seahorses are known to associate with environmental features at small scales, often choosing to use either unusual substrata that are rare (e.g. fishing line, shark nets), that exhibit distinctive morphology suitable for grasping, or that are different from the surrounding matrix (Foster & Vincent 2004a).

An understanding of benthic habitat associations in seahorses is important for management because all species were recently listed on CITES Appendix II in recognition of threats posed by a high volume international trade (Foster & Vincent 2005). The habitat associations of tropical seahorses (which comprise 70 % of the genus *Hippocampus*) are poorly understood and juvenile rearing grounds remain unknown for most of the world's 34 seahorse species. Research was therefore focused on the habitat associations of the mid-sized, tropical tiger tail seahorse, *Hippocamus comes* Cantor 1850*,* which inhabits shallow Asian waters (Lourie et al. 2004; Perante et al. 2002) and is classified as "Vulnerable" by the World Conservation Union (IUCN 2006) due to heavy exploitation and habitat degradation.

The aim of the present research was to document which benthic communities in coral reef ecosystems were used by juvenile and adult seahorses and to determine whether *H. comes* exhibits ontogenetic shifts in macro- (10-100 m) and microhabitat (1-10 m) associations. The study further investigated whether there was evidence of preference for particular microhabitat, and whether this was related to reef zone or life history phase.

Of particular interest was locating the principal benthic habitat used by small juvenile cohorts, which remains to be comprehensively documented for any

Hippocampus species. References to juvenile seahorses that presently exist in the literature pertain either to planktonic young (Kanou & Kohno 2001; Vandendriessche et al. 2005), or to animals close to maturity (Curtis & Vincent 2005), likely to have settled some months earlier, perhaps outside of adult habitat (Bell et al. 2003; Martin-Smith & Vincent 2005). At present, ontogenetic shifts in the habitat use of seahorses are inferred from the dearth of juveniles in areas inhabited by adults.

METHODS

Study Species

Hippocampus comes occurs in Indonesia, Malaysia, Singapore, Thailand and Vietnam (Lourie et al. 2004) with most sightings from the central Philippines. Adult *H. comes* live at depths of 0.5–10 m (Morgan & Lourie 2006), with rare sightings at 20 m (Kuiter 2000). Large individuals are found mainly on coral reefs (Perante et al. 2002) or associated with structures in seagrass beds (J. Anticamara, pers. comm.). Anecdotal information suggests that juveniles can be found in seasonal macroalgal beds (Perante et al. 1998). Holdfasts grasped by seahorses as anchor points commonly include branching structures such as sponges, bifurcating corals, sunken branches, and artificial rope or dock structure (Pajaro et al. 1997). All studied seahorses appear to be monogamous within breeding events and most maintain long term pair bonds (Foster & Vincent 2004a). In *H. comes*, prolonged monogamy in reproductively synchronized pairs has been observed over periods as long as 21 months, with occasional sightings of trios and foursomes (Perante et al. 2002).

Study System

The study was conducted from January to April, 2003 on the Danajon reef system north of Bohol province in the central Philippines (Fig. 1). Surveys were timed to correspond with the peak catch of juvenile seahorses (Project Seahorse, unpublished data) and took place near four islands called Cataban, Saag, Sagasa and Mahanay in the northern portion of the Danajon Bank reef. This double barrier system runs parallel to the northern and western coasts of Bohol, for about 145 km (Pichon 1977) and comprises many small islands and atolls separated by water 10-14 m deep with occasional channels to 28 m (Green et al. 2000). The area is subject to mixed semi-diurnal tides and is sufficiently sheltered by surrounding island provinces that waves rarely exceed a height of 1 m.

Benthic Habitat Surveys

Manta tows – rapid visual surveys by a towed in-water observers - around nine islands identified seven main patterns of zonation (five biotic, two abiotic) in the Danajon Bank following the methods described in English et al. (1997). Based on the knowledge of local fishers and earlier research showing low densities of *H. comes* in certain reef zones (Perante et al. 2002; Perante et al. 1998), four biotic communities were selected for further investigation (coral reef , wild macroalgal bed, farmed macroalgal bed, seagrass meadow). One unfished coral reef zone was surveyed in a marine sanctuary on Cataban Island, as an area without fishing impacts; such opportunities were not available for the other three benthic communities. Mangrove habitats were considered for inclusion in the study, but high turbidity and shallow waters made surveying logistically intractable.

Monthly surveys of benthic cover in macroalgal habitats and single surveys in coral reefs and seagrass were undertaken at each island. In coral reef communities, cover was not quantified in each survey because of negligible coral growth over the three month sampling period. At each island, ten transects were laid haphazardly parallel to depth contours in each of the four macrohabitats. Farmed macroalgal beds were sometimes too small for ten transects and irregularly shaped; here transects were laid opportunistically as space allowed (n = 15, 18-490 m^2). Transect location was recorded using a GPS unit (accurate to 7

m) and benthic cover was quantified using S.C.U.B.A. or snorkel (depending on depth), in one randomly chosen 50 m stretch on each tape.

Using standard line intercept methods (LIM) modified from the Australian Institute of Marine Science (English et al. 1997), benthic habitat was recorded to the nearest 5 cm in 53 morphological categories. For example, reef corals were grouped into functional classes that included branching coral, foliose coral, massive coral, and submassive coral, *etc*. These classes were grouped for various analyses.

Seahorse Surveys

Hippocampus comes is most easily seen at night, when it rises up on holdfasts (Morgan & Lourie 2006). Therefore, transects originally laid and surveyed for benthic cover during daylight, were searched for seahorses between 00:50 and 05:45. Both macroalgal macrohabitats and coral reef were surveyed monthly, over three months for *H. comes*. Seagrass communities were surveyed only during the first round of monitoring in February because the absence of young supported consistent reports from fishers that seahorses were not found in homogeneous stands of seagrass (C. Socias, pers. comm.). Two experienced seahorse fishers (>5 years fishing each) visually counted *H. comes* while breath-hold diving by the light of pressurized kerosene lanterns. Searches were standardized to 20 minutes per transect and covered 3 m on both the left and right of submerged tape measures (belt transect area = 600 m^2: 2 people x 3 m each x 100 m). Over 49 nights, a total of 393 transects were surveyed for seahorses, covering a total area of 230 173 m^2.

For each *H. comes* sighted, data were collected on the animal's depth, type of holdfast (always to genus, and species where possible), height on the holdfast, overall holdfast height, sex (male, female or undefined), reproductive status, head length, tail length and trunk length (Lourie 2003): animals were then returned to their original holdfasts. Male reproductive status was determined by the presence of a mature brood pouch and female reproductive status was defined by the presence of an egg bulge in the ventral region of the terminal trunk segment (Perante et al. 2002). Prior to analysis, and to facilitate comparison with other research, straight standard lengths (SLs) were converted to curved standard lengths (SLc) using the equation (regression, $SLc = 1.0037\ SLs + 2.7781$, $n = 110$, $p<0.001$) (L. Brady, unpublished data). The transition between juvenile and adult was defined at 105.4 mm SLc, corresponding to observed brood pouch development and the smallest male carrying young seen in dissections of $n = 71$ *H. comes* from the study area (L. Brady, unpublished data).

Data Analysis

Two multivariate approaches, implemented in PRIMER 5.1™ (Clarke & Warwick 2001) were used to verify the validity of *a priori* sample stratification by community. Hierarchical cluster analysis, based on Bray-Curtis similarity coefficients (group averaged method) defined substratum similarities in cover categories among benthic transects ($n = 389$). Clusters were corroborated by non-metric multidimensional scaling (nMDS). Outside the four main community clusters, a single seagrass transect formed a fifth cluster that was grouped with its next most similar cluster, containing all other seagrass transects. The magnitude of differences in substrate assemblages among communities was tested using one way ANOSIM permuted 999 times. The output statistic (global r) approaches one when a factor, such as community type, divides transects into distinct, non-overlapping groups.

Ranking methods were used to test whether abundance differed significantly among macrohabitats because area-standardized densities, based on counts, were strongly non-normally distributed. Freidman's tests, non-parametric analogues of repeated measures analysis of variance, are designed to examine the relative rank of samples that are tied in some way. In this case, islands were blocked, to account for the possible effect of location. Densities of *H. comes* on all transects within each macrohabitat at each location were averaged and ranked within location. The analysis was repeated for juveniles and for adults. Multiple pairwise comparisons, examined ranked differences in density between macrohabitat pairs within life stage (e.g. between juvenile densities in coral reef and wild macroalgal beds), using a non-parametric analogue of the Tukey test (Zar 1996).

When microhabitat use was examined by seahorse size, holdfasts categorized to the species level were grouped into six broader categories: coral, macroalgae, seagrass, sponges, artificial structure, abiotic structure and "other". Since more transects were surveyed in coral crest habitat than elsewhere, computer-generated random numbers were used to re-sample an equivalent number of transects for seahorses within all community-island combinations.

Microhabitat preference (as opposed to use) was examined using a ratio index. The ratio index (U_{kn}/A_n) reasons that an organism's choice of habitat should be a function of how frequently a given substratum, expressed as a percentage of total use (U_{kn}), is used relative to its availability (A_n), where k = life history stage, n = substratum. A ratio of 1 indicates that habitat is used in proportion to its availability, >1 that habitat is used more than expected relative to its availability (choice) and <1 and less than expected (avoidance).

The aggregation of seahorses on transects was assessed using three indices of dispersion: Green's coefficient, the standardised Morisita's index, and the variance to mean ratio (Krebs 1989). Results are reported only for Green's coefficient as patterns were robust to all methods, and Green's coefficient is nearly independent of population density and sample size (Myers 1978). Green's coefficient of dispersion (Gc) is calculated as $Gc = [(s^2 x^{-1})-1][\Sigma(X-1)]^{-1}$, where s^2 = sample variance, x = sample mean and X = total number of individuals per sampling unit. This index is positively biased at low sample sizes (i.e. <50), so Gc values from Cataban sanctuary (n = 30 transects) should be treated with some caution. The Ip index associated with the standardized Morisita's index was used to confirm 95 % confidence intervals (at +0.5 and -0.5) around principle patterns of aggregation (Smith-Gill 1975).

RESULTS

Seahorse Abundance and Distribution

A total of 328 seahorses were found over all surveys, made up of 189 juveniles (58 %) and 139 adults (66 males and 73 females) (42 %), for an overall density of 1.43 X 10^{-3} individuals m^{-2} or approximately 3 seahorses per 2000 m^2. The smallest recorded individual measured 26.7 mm SLc, while the largest individual was 210.3 mm SLc (Table 1). Juveniles averaged approximately 90 mm less in total standard length than adults. The overall sex ratio among adults in the population was effectively equal (two-sample t-test, n = 139, $p>0.05$).

Seahorses were found on 40 % of all transects (n = 157). Abundance was strongly non-normally distributed and frequency decreased in a negatively exponential manner with increasing seahorse counts per transect. Fifty one percent of occupied transects had one individual, while one transect was inhabited by nine individuals. All surveyed individuals were found grasping holdfasts.

Reef Zones

Multivariate analyses of similarity (cluster analysis and non-metric multidimensional scaling) confirmed significant differentiation among the four main reef zones or macrohabitats used as sampling strata (ANOSIM: n = 389, p = 0.001, r = 0.967) (Fig. 2). Ninety-nine percent of transects (356/359) assorted correctly into these groups, defined visually at 45 % (Bray Curtis) similarity. Zonation changed with depth. Shallow reef flats were inhabited by seagrasses

(*Thalassia hemprichii, Enhalus acoroides*), the terminal edge of reef flats abutting the crest was generally occupied by wild (*Sargassum* spp.) or cultured (*Eucheuma denticulatum* or *Kappaphycus alverizii*) macroalgal beds, and the reef crest, by coral colonies. Benthic structure on unfished coral transects was representative of fished sites (Fig. 2).

Biotic cover made up a significant portion of the substratum in all communities, from a high of 59.8 % on coral crests, to a low of 36.4 % in seagrass communities. In all beds but seagrass, live cover exceeded the abundance of abiotic substratum. In both wild and farmed macroalgal beds, the group dominants comprised 45-50 % of the total cover, whereas in coral reef and seagrass, dominants comprised 30-35 % of total cover (Table 2). Coral reefs were the only community where another group, sponges, comprised more than 10 % of the overall substratum.

Macrohabitat Use

Seahorse densities differed significantly among corals, wild macroalgal beds and farmed macroalgal beds for both juveniles (Friedman's test, df = 3, 3, $p<0.05$) and adults (Friedman's test, df = 3,3, $p<0.05$) (Fig. 3). Seagrass meadows and the coral reef reserve were not included in the analysis because of low sample numbers. Juveniles were most abundant in wild macroalgal beds, where they were twice as dense as in fished coral reef (multiple comparisons, v, $k = \infty, 3$, $\alpha = 0.05$) (Fig. 3, Table 1). In contrast, mean adult density was greatest on coral reefs and in wild macroalgal beds (Fig. 3, Table 1). Mature animals were sparse in farmed macroalgae, with densities half as great as adults in the other two macrohabitats (multiple comparisons, v, $k = \infty, 3$, $\alpha = 0.05$) and approximately one fourth the density of juveniles in wild macroalgal beds.

Mean adult size increased from farmed macroalgal beds, to wild macroalgal beds, to fished coral reef and then to the unfished coral reef reserve

(Table 1), commensurate with increases in benthic community richness. This relationship was significant when plotted within island-location combination (e.g. Cataban-wild macroalgae, Sagasa-fished coral reef) where adults were present (Pearson product-moment correlation, df = 10, $p<0.05$) (Fig. 4). Mean juvenile size did not show comparable patterns with macrohabitat (Table 1). Depth varied too little among habitats (which are also natural strata in reef zonation) to confound the relationship between adult size and habitat meaningfully (regression, df = 1,333, $R^2 = 0.0136$, $p = 0.032$) and percentage biotic cover could not be used to predict either juvenile or adult density ($\text{regression}_{\text{juv}}$, df = 1,387, $p>0.05$; $\text{regression}_{\text{adult}}$, df = 1,387, $p>0.05$).

Microhabitat Use

A total of 22 species/genera were used as holdfasts, with the type and number of holdfasts varying between juveniles and adults. Across all reef zones, there was a significant ontogenetic difference in the morphology of holdfasts used by juveniles versus adults (chi-squared test of independence, df = 6, n = 328, $p<0.001$). Juveniles showed marked use of a single foliose holdfast, *Sargassum* spp. (51 %, Table 3), while adults showed a much more even spread in their use of substrata, mainly grasping branching or strap-like structures (Fig. 5). The notable proportion of smallest young (40 %) apparently using sponges, arose from the unusual use of two poriferan species (*Haliclona korema* and *Callyspongia diffusa*) at the Mahanay reef site. With this site excluded, macroalgal use in the smallest size class was 69 %. At a size threshold of 120-150 mm SLc, macroalgal use dropped markedly from levels well above 50 % to comprise ca. 10 % of holdfasts in all larger individuals. At the same time, the percentage use of other holdfasts, particularly sponges, increased.

At the scale of holdfasts, juveniles generally used fewer types of benthic structures than adults (Fig. 6). On coral reefs, the greatest diversity of substrata were used as holdfasts (n = 19), and juveniles used fewer types of holdfasts (n =

12) than adults (n = 15). Five of the six most common juvenile holdfasts were sponges, whereas adults principally used the branching coral *Porites sp*. (24.6 %) as well as sponges [*Clathria fasciculata* (19.3 %) and *Pellina carbonaria* (10.5 %)]. In wild macroalgal beds, 13 identified substrata were used as holdfasts, with fewer types of holdfasts used by juveniles (n = 6) than adults (n = 10). Juveniles used *Sargassum* spp. in >90 % of sightings (Fig. 6). In contrast, adults used *Sargassum* spp. approximately half as often (47.4 % of sightings) and also exhibited considerable dependence also on the tall strap-like seagrass, *E. acoroides* (28.1 %). In farmed macroalgal beds, only six types of holdfasts were used; 4 by juveniles and 5 by adults. *Eucheuma denticulatum* and twine were most commonly used by juveniles (65.2 %, 17.4 %) and adults (41.67 %, 25.0 %) respectively. Tall seagrass (*E. acoroides)* was also used by adults (25 %).

Larger seahorses used taller holdfasts (regression, df = 1,332, $p<0.001$) but showed no meaningful tendency ($R^2 = 0.035$) to change their position by grasping holdfasts at relatively greater heights (position on holdfast: height of holdfast) as they increased in size (regression, df = 1,333, $p<0.01$).

Microhabitat Preference

Of the 53 surveyed substrata, a total of 11 types of cover were used as holdfasts (Table 3). Commonly used holdfasts in more than one community included branching sponges, the brown algae *Sargassum* spp. and the seagrass *E. acoroides*. Both adult and juvenile seahorses showed high preference ratios for rare microhabitat, such as submerged branches and rope, where these were present.

Adult seahorses often preferred to grasp large/ tall structures, distinctive from the predominant matrix in a given community. For example, in coral reefs, rare branching sponges, branching corals and submerged wild tamarind branches (*Leucaena leucocephala*) were preferred. In macroalgal communities, infrequent patches of *E. acoroides* were often used by adults. In contrast to adults, most juveniles were found in macroalgal beds and used the dominant substrata such as *Sargassum* spp. and *Kappaphycus* spp. in proportions equivalent to, or only slightly greater than, their availability (Table 3). Some substrata showed high preference values by juveniles, but were used infrequently (e.g. branches, rope, Hydrozoa) (Table 3).

Aggregation

All three tested indices of dispersion showed that regardless of life history stage, seahorses exhibit aggregated distributions. Over all reef zones, clumping was more prominent in adult than juvenile seahorses ($GC_{juv} = 2.10$, $GC_{adult} = 2.26$), and Ip values >0.5 indicated that animals were 95 % likely to be significantly clumped for both life stages ($Ip_{juv} = 0.504$, $Ip_{adult} = 0.506$). Aggregation varied among reef zones where the most closely associated adults ($GC_{adult} = 3.92$) were found on the unfished coral reef within the marine reserve. Among reef zones, aggregation was greatest in coral environments, less in wild macroalgal beds, and least in farmed macroalgal beds (corals, $GC_{juv} = 2.44$, $GC_{adult} = 2.13$; wild macroalgae, $GC_{juv} = 1.90$, $GC_{adult} = 2.02$; farmed macroalgae, $GC_{juv} = 1.66$, $GC_{adult} = 1.37$). Adults were more aggregated than juveniles in wild macroalgal beds and the unfished Cataban sanctuary. In fished coral reef and harvested macroalgal beds, adults were less aggregated than juveniles.

Crypsis

Seahorse colour shifted with life history stage (chi-squared test of independence, df = 3, n = 314, $p<0.001$). While juvenile, many animals showed light brown colouration, or shades of pale brown, yellow, or gray; well camouflaged in *Sargassum* spp. beds. As animals grew, they increased pigmentation, taking on more uniform mid-brown tones that ranged to dark brown and black. Colours adopted by adults included yellow and distinctive black and yellow tiger-striping along the dorsal surface. Colouration did show minor sex differences, driven by an apparent female-bias in yellow adults (77 % female, n = 30 yellow adults) (chi-squared test of independence, df = 3, n = 140, $p<0.05$). In a relative sense, tiger-striping was the pattern most reliably associated with adults (90 % adult, n = 55), although in an absolute sense, almost the same number of brown adults were seen (n = 48), with brown being the most common colour overall (56 %) (Fig. 7).

DISCUSSION

This research represents the first comprehensive exploration of ontogenetic shifts in benthic habitat associations within the genus *Hippocampus*, providing evidence that *H. comes* is a reef fish that uses wild macroalgal beds as rearing habitat. Juveniles occurred principally in macroalgal communities, using *Sargassum* spp. holdfasts, whereas adults were found on coral reefs and in macroalgal beds, using a wide diversity of holdfasts. Despite unusual morphology, seahorses decrease microhabitat selectivity with size, like other teleosts. Shifts in holdfast use occur at a distinct size threshold, which along with increasing aggregation and shifts in colouration, may relate to reproductive behaviour. The present findings provide useful information for the management of *H. comes*, particularly the identification of areas used as juvenile rearing grounds and by large, fecund adults.

Macrohabitat Use

A limited amount is currently known about the habitat use of tropical seahorses which comprise most of the genus *Hippocampus*. Adult *H. barbouri* Jordan and Richardson, 1908, occur in association with the tall strap-like seagrass *E. acoroides* but seldom on coral reefs (A. Maypa, unpublished data), while *H. comes* have been recorded from communities with varying degrees of live coral, dead coral, seagrass and macroalgae (*Sargassum* spp.) (Perante et al. 2002). In Peninsular Malaysia, surveys of *H. kuda* Bleeker 1852a, in shallow water showed animals using structures comparable to *H. comes* holdfasts*,* including seagrass (*E. acoroides)*, macroalgae (*Caulerpa* sp.), mangrove roots, fish nets or cages, but not corals or sponges. In contrast, trawl-catch of deeper water species (*H. kelloggi* Jordan and Snyder 1902 , *H. spinosissimus* Weber 1913*, H. trimaculatus* Leach 1814) also included octocorals, macrophytes and sponges (Choo & Liew 2003).

The association of juvenile *H. comes* with macroalgal habitat is consistent with what has been reported from other seahorses species. However, in most populations, young are sighted infrequently making it difficult to interpret (particularly in the absence of size distribution and maturity information) whether juveniles are recent recruits to rearing grounds, or sub-adults occupying adult habitat. For example, in a cold-water population of *H. breviceps* Peters, 1869, 25 % of animals sighted were juveniles in a mixed-macroalgal bed (Moreau & Vincent 2004). Similarly, a *H. reidi* Ginsburg 1933, population, composed of 37 % juveniles, occupied a pier environment with macroalgae, sponges and encrusting invertebrates (Dias & Rosa 2003). In temperate populations of *H. guttulatus* (Curtis & Vincent 2005) and *H. abdominalis* Lesson 1827 (Martin-Smith & Vincent 2005), sub-adult juveniles share macroalgal habitat with adults. The smallest juveniles are planktonic, but an intervening suite of size classes are neither regularly present in plankton tows, nor found regularly in benthic surveys (Curtis & Vincent 2006; Perez-Ruzafa et al. 2004). Regardless of species, habitat associations should be investigated during known periods of recruitment.

The use of macroalgal beds by juvenile seahorses is unusual among tropical reef fishes, that tend to use seagrass meadows, or mangrove roots as sub-adults (Mumby et al. 2004; Nagelkerken et al. 2001). In temperate reef systems, however, macroalgal beds have been documented as important nursery habitat for the young of rocky reef-associated species (Carr 1989; Holbrook et al. 1990; Nelson 2001). Macrophytic structures provide complex three dimensional space for shelter, which is characteristic of habitats known to harbour high fish biomass (Friedlander 2001; Heck et al. 2003). Recently, the young of commercially important tropical species such as groupers have also been found in macroalgal beds (Dahlgren & Eggleston 2001; Jenkins & Wheatley 1998; Light & Jones 1997).

High densities of *H. comes* young in macroalgal beds may result from higher settlement rates by young in these areas, with later movement into reef habitat, or from lower predation on young in foliose algal beds than in other habitats. Higher survivorship in macroalgal beds may also be linked to the distribution of prey populations (Kendrick & Hyndes 2005). Survivorship of small reef fishes is known to be poorly (Levin 1993) and greatly (Beukers & Jones 1997) influenced by predation in some tropical habitats, but is not well understood in macroalgal environments (Rossier & Kulbicki 2000). Marking and exclusion studies could help distinguish mechanisms driving the observed ontogenetic shifts in habitat associations of *H. comes* and explore whether macroalgal beds constitute a “true nursery” by contributing proportionally high numbers of individuals to adult populations (Beck et al. 2001).

The presence of small *H. comes* (30-50 mm) on the benthos does undermine a possible hypothesis; that large sub-adult *H. comes* (50-100 mm) recruit directly from the plankton into adult habitat, thought to occur in other seahorses (Curtis & Vincent 2006). The absence of a meaningful relationship between seahorse size and depth, and the location of macroalgal beds in shallow water to the landward (shallow) side of coral crests, also makes it unlikely that very small seahorses (15-30 mm) recruit to deep-water bottoms, then migrate to shallower areas.

Community differences in macrohabitat features were related to the distribution of the largest animals in the study population. The largest seahorses were found in the habitats with the greatest number of cover “types”. Our survey method categorized benthic cover by a combination of taxonomy and morphology (e.g. branching coral), rather than by taxonomy alone (e.g. *Porites* spp.).

Therefore, our index should have a clearer relationship with parameters such as rugosity and structural diversity than a more species-specific richness index. More morphologically rich environments may provide increased opportunities for foraging, or more or better refugia from predation, both natural and anthropogenic (Orth et al. 1984). Particularly for large adults that are targeted for trade, it may be important to have access to abundant and substantial reef structure that cannot be easily moved or searched by fishers.

Microhabitat Use and Preference

Hippocampus comes, like many teleosts, alters its microhabitat use with size (Werner & Gilliam 1984). The transition from the use of macroalgal and sponge holdfast by juveniles to the diverse range of holdfasts used by adults is accompanied by increased aggregation and decreased crypsis. Such transitions may be explained by considering at least three, nonexclusive factors that affect fitness: prey availability (growth), predator avoidance (survival) and reproduction.

One important aspect of habitat is that it must provide prey items needed for growth: as prey choice changes with size, so may habitat associations. The in situ feeding ontogeny of tropical seahorses is not known, but in culture, juveniles are given rotifers and copepods then fed crustaceans such as mysids and *Acetes* at larger sizes (Choo & Liew 2006). The juvenile preference for copepods has also been seen in temperate seahorses (Texeira & Musick 2001). To determine whether foraging drives ontogenetic shifts in the habitat associations of *H. comes*, it will be necessary to determine a) the diet composition of juvenile and adult *H. comes*, b) how prey availability differs among tropical habitats and c) if seahorses' foraging success depends on the structure of macroalgal beds versus coral reef environments (James & Heck 1994).

Size-related changes in vulnerability to predation are known to influence habitat use by marine fishes (Sogard 1997). In *H. comes,* nocturnal crypsis decreases with size as larger individuals associate with microhabitat in a manner that provides poor camouflage. At small sizes, *H. comes* are spiny and generally brown, with mottled patterns that make them difficult to distinguish from *Sargassum* fronds. Adults develop darker brown pigmentation, usually with yellow saddles or stripes on the dorsal surface, or may also be yellow. Adult colours often contrast with the appearance and form of nocturnal holdfasts that include "ropy" pink or orange sponges (*C. fasciculata*), submerged branches or yellow branching corals heads (*Porites sp*.). By day, *H. comes* move beneath, or to the base of such structures, where their colouration affords camouflage in patchy shadows and dappled light.

Reproductive opportunity may also influence habitat occupancy by adult *H. comes*. Here three lines of argument were considered that indicate that, in seahorses, the use of prominent substrate may promote the establishment or maintenance of pair bonds seen in the genus (Foster & Vincent 2004a) and in other small tropical fishes (Hobbs & Munday 2004; Munday et al. 2002; Patton 1994; Wong et al. 2005). (1) The transition in habitat use occurred at 120-150 mm SLc, just above the size when 50 % of reproductive males are pregnant (Lr = 116 mm, Chapter 4) and well beyond the size at which *H. comes* are known to mature physiologically (Lm = 96 mm) (Morgan & Lourie 2006). Therefore changes in associations align allometrically with brooding. (2) As seahorses grew, they were more likely to be found aggregated, particularly in the reserve site. In wild populations of *H. comes*, males and females have exhibited at least social and perhaps sexual monogamy of pairs that have endured up to 21 months (Perante et al. 2002). Association with aggregation sites or core areas by suspected mates has also been noted in *H. breviceps* Peters 1869 (Moreau & Vincent 2004) and *H. whitei* Bleeker 1855 (Vincent et al. 2005). (3) Adults were more visible than juveniles, with larger animals choosing unusual holdfasts and moving to more prominent positions off the bottom at night, when they have been observed in pairs (Perante et al. 2002). Increased reproductive efficiency, believed to promote monogamy in seahorses, is a logical outcome of associating with specialized habitat features in low density populations (Whiteman & Côté 2004). Congeners also become more prominent during reproduction, engaging, for example, in colourful, active and lengthy courtship displays (Vincent & Sadler 1995).

Therefore, transitions in the use of microhabitat (and perhaps macrohabitat) that align with brooding rather than physical maturity, increased aggregation, and the adoption of behaviour that increases prominence, are all consistent with a tradeoff that favours investment in reproduction against avoidance of predation with increasing size. Such trade-offs have been noted within life history stage in the family Syngnathidae, but not among age or size stages (Fuller & Berglund 1996).

Conservation Implications

Hippocampus comes in the central Philippines faces pressures from targeted extraction, destructive fishing (and other forms of habitat damage) and macroalgal farming. Limited data here suggest that aggregation among reproductive adults is diminished in fished and highly disturbed sites, where capture of one adult will also curtail the reproductive output of its partner. Further, blast-fishing damages benthic habitat and encourages phase-shifts from hard coral communities to soft corals and macroalgal beds (Hurtado & Ragaza 1999). This could augment the recruitment of *H. comes* juveniles, but leave adults with fewer appropriate holdfasts on intact coral reefs where breeding occurs.

In the Danajon Bank, *Eucheuma* spp. and *Kappaphycus* spp. macroalgae are farmed above wild macrophytes and corals; which are either cleared when farms are established, or shaded by the suspended vegetation. Low densities of *H. comes* in farmed algal beds suggest that these represented a poor habitat-substitute for wild macroalgae, perhaps due to the non-foliose morphology of farmed species, because of regular harvest disturbance, or to some combination of both. Juvenile rearing grounds will also be disturbed by the cutting of wild *Sargassum* beds which are used to make "kelp powder" for export (Hurtado & Ragaza 1999). In the face of declining fish catches, macroalgal farming is expanding in many parts of the Philippines. The effects of such expansion on the habitat needs of seahorses and other wild food fishes deserve immediate research.

To focus conservation and management effort, population dynamics of *H. comes* should be modeled in the context of habitat availability (Levin & Stunz 2005). If the juvenile phase were identified as limiting, macroalgal habitat could be added to the many marine reserves in the region, most of which are focused on coral reefs. Should the adult stage prove limiting, then morphological richness could be used to identify management areas with large spawners, known to contribute disproportionately to the maintenance of populations, by giving birth to more young, young in better initial condition and young with genes that favour survivorship (Froese 2004). Ideally, fishing communities would be interested in developing marine reserves encompassing all reef zones from the inshore to (at least) crests. Adopting this type of precautionary approach would maintain physical and developmental pathways (ontogenetic connectivity) for *H. comes* and many other marine organisms of economic importance. It would also provide insurance against spatial and temporal shifts in limiting habitat arising from variable disturbance regimes.

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Table 1. Density and size (SLc) ± S.D. of *Hippocampus comes* sighted during surveys. Densities are given in individuals m^{-2} X 10^{-4}. Sample size (n) gives the number of juveniles or adults in particular macrohabitats. Abundances should not be compared directly because sample numbers (transects) varied by macrohabitat.

Macrohabitat	**Juvenile**				**Adult**			
	n =	**Density**	**Mean SLc (mm)**	**SLc range (mm)**	**n =**	**Density**	**Mean SLc (mm)**	**SLc range (mm)**
Coral reef (fished)	52	7.28 ± 1.57	64.1 ± 17.6	26.7-100.6	53	7.42 ± 1.48	166.9 ± 25.6	107.1-201.9
Wild macroalgae	104	14.6 ± 1.92	71.8 ± 19.9	37.1-105.1	57	7.98 ± 1.50	159.1 ± 29.8	105.4-210.3
Farmed macroalgae	22	4.31 ± 1.19	76.8 ± 17.0	46.9-103.4	12	3.28 ± 1.24	144.2 ± 25.7	114.9 – 195.5
Seagrass	0	0 ± 0	n/a	n/a	1	0.042 ± 0.42	133.4 ± n/a	n/a
Coral reef (unfished)	11	6.11 ± 1.97	69.2 ± 14.8	48.3 - 94.4	16	8.89 ± 4.22	174.1 ± 21.8	129.1-202.5
Total	189	8.02 ± 0.84	70.1 ± 19.0	n/a	139	6.10 ± 0.78	162.3 ± 27.8	n/a

Table 2. Percentage composition of reef zone community clusters, defined at 45 % similarity by Primer™ cluster analysis. Data in 53 cover classes were consolidated into seven broad taxonomic categories: C, corals; SP, sponges; MA, macroalgae; SG, seagrass; O/B, other/branches; ART, artificial substratum; AB, abiotic substratum. Composition gives the percentage of each community composed of the seven broad cover categories. Each community was named after its dominant biotic taxonomic group. N gives transect numbers per community. Mean richness describes the average number of unconsolidated morphological cover classes observed in a given community. Transects from the marine reserve were not included in the analysis (n = 30).

Community				**Composition**					**Mean Richness**	**% Positive classification**
	n =	**% C**	**% SP**	**% MA**	**% SG**	**% O/B**	**% ART**	**% AB**		
Coral crest	120	34.8	12.7	7.3	1.1	3.9	0.01	40.2	17.30	100
Wild macroalgae	118	9.7	3.1	44.6	2.0	1.3	0.02	39.3	14.52	97*
Farmed macroalgae	81	5.1	1.0	47.5	9.4	1.7	0.05	35.2	9.47	100
Seagrass A	39	0.1	0.2	4.4	31.4	0.5	0	63.4	8.95	100
Seagrass B	1	0	0	1.0	97.9	1.1	0	0	7.0	100

* Three of n = 118 wild macroalgal transects grouped with farmed macroalgal transects

Table 3. Microhabitat preference given as the preference ratio (Ip) index (U_{kn}/A_n) of mean percentage use to availability for all substrata utilized by adult and juvenile seahorses within each community. Microhabitats used by >/= 5 animals are given in bold. N values at the top of columns give sum totals for all rows below.

Community	**Coral**		**Wild macroalgae**		**Farmed macroalgae**		**Seagrass**	
Holdfast	**Adult** Ip (57)	**Juv.** Ip (52)	**Adult** Ip (57)	**Juv.** Ip (104)	**Adult** Ip (12)	**Juv.** Ip (23)	**Adult** Ip (1)	**Juv.** Ip (0)
Submerged branches (*Leucaena leucocephala*)	**3211.4 (5)**		1948.1 (4)	533.8 (2)				
Branching coral (*Seriatopora* spp, *Porites* spp.)	**2.5 (17)**		12.2 (4)					
Dead coral	50.4 (1)		55.7 (1)					
Seagrass (*Enhalus acoroides*)			**82.6 (16)**		7.0 (3)	2.4 (2)		
Hydrozoan (*Lytocarpus philippinus*)	117.8 (1)	128.0 (1)						
Farmed macroalgae (*Kappaphycus/Eucheuma* spp.)	48.0 (2)	79.0 (3)		1.2 (2)	**0.8 (5)**	**1.2 (15)**		
Rope or twine	367.0 (4)	100.6 (1)			3694.5 (3)	2570.1 (4)		
***Sargassum* spp**.	1.3 (1)	**7.1 (5)**	**1.2 (27)**	**2.2 (91)**		1.0 (1)	122.7 (1)	
Soft coral (*Isis hippuris*)		2.1 (2)						
Sponge (unidentified)			51.3 (2)		246.3 (1)			
Branching sponges (many species)	**7.6 (26)**	**12.8 (40)**	4.5 (3)	**7.4 (9)**		27.2 (1)		

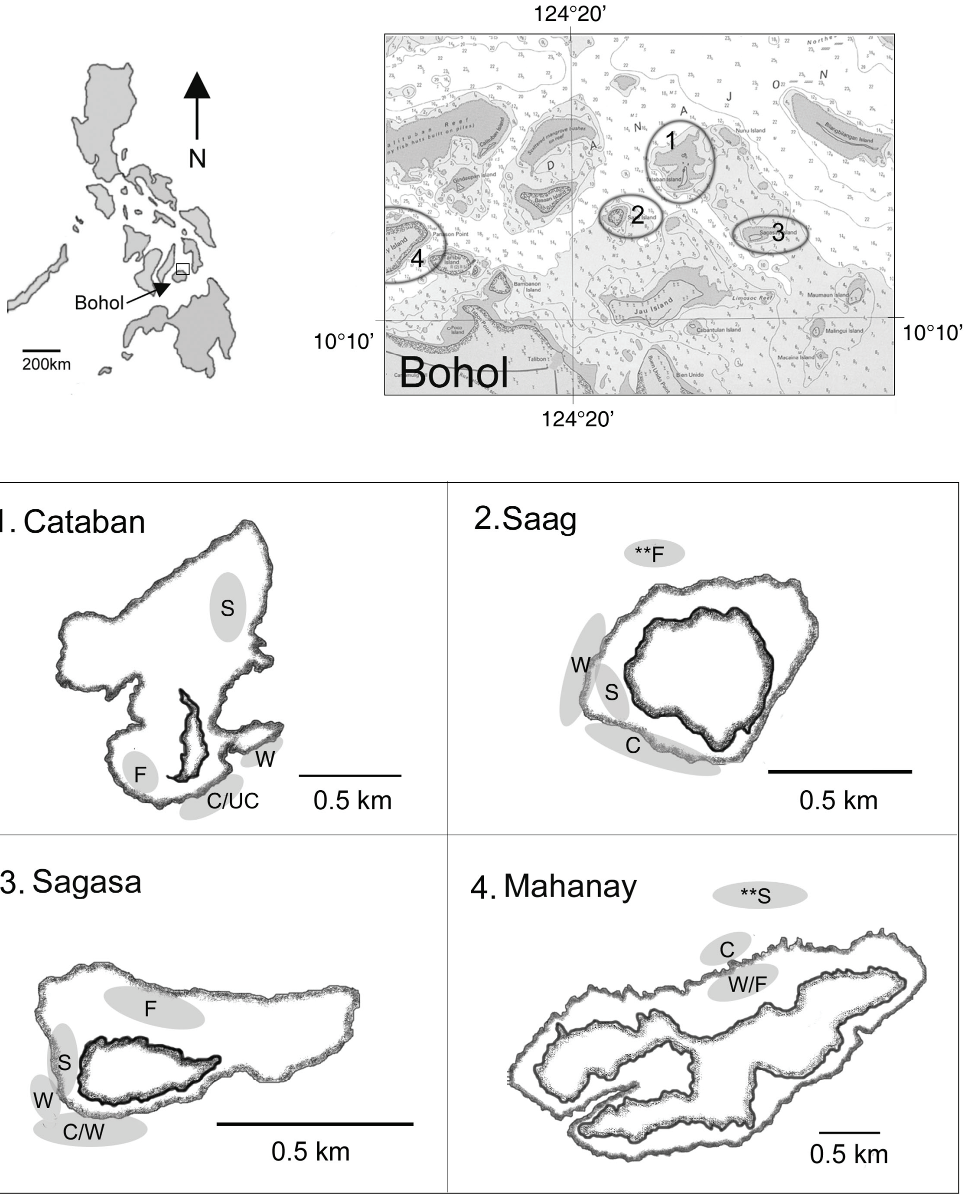

Figure 1. Location of study sites, Bohol Province, central Philippines: (a) Cataban Island (10°13.75’N, 124°23.36’E), (b) Saag Island (10°12.50’N, 124°20.97’E), (c) Sagasa Island (10°12.05’N, 124°25.75’E), and (d) Mahanay Island (10°12.50’N, 124°14.23’E). Reef zone communities at each island are given by initials: C, coral reef; S, seagrass beds; W, wild macroalgal beds; F, farmed macroalgal beds; UC, unfished coral reef (Cataban Island only); **, habitats located on atolls adjoining main island sites.

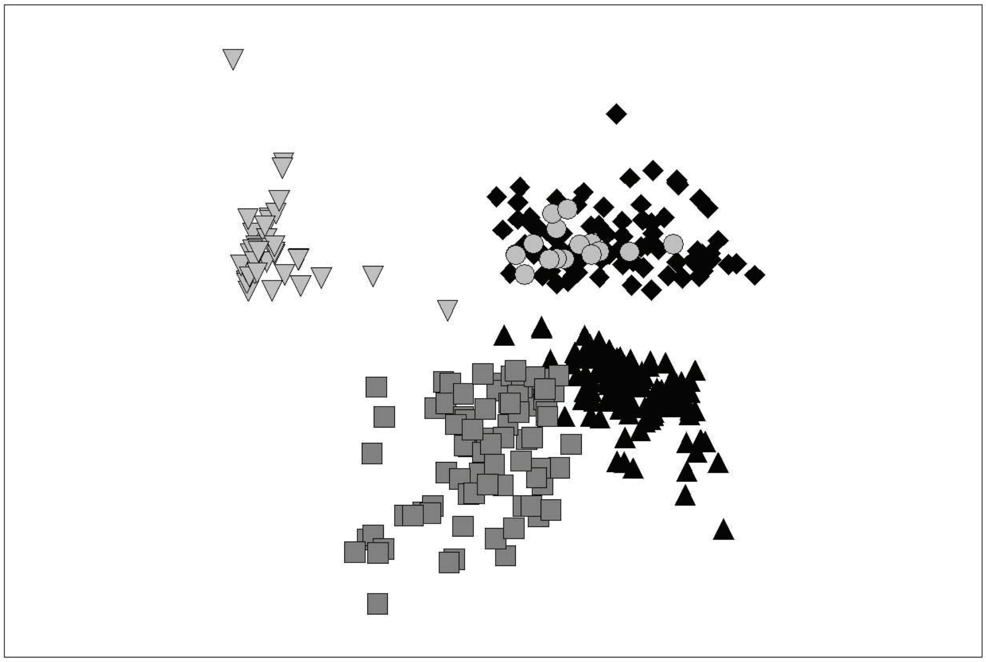

Figure 2. Non-metric multidimensional scaling analysis showing stratification of the reef zone communities surveyed [(▼), seagrass; (■) farmed macroalgae, (▲) wild macroalgae; (◆) fished coral reef; (●) unfished coral reef reserve]. Stress = 0.1

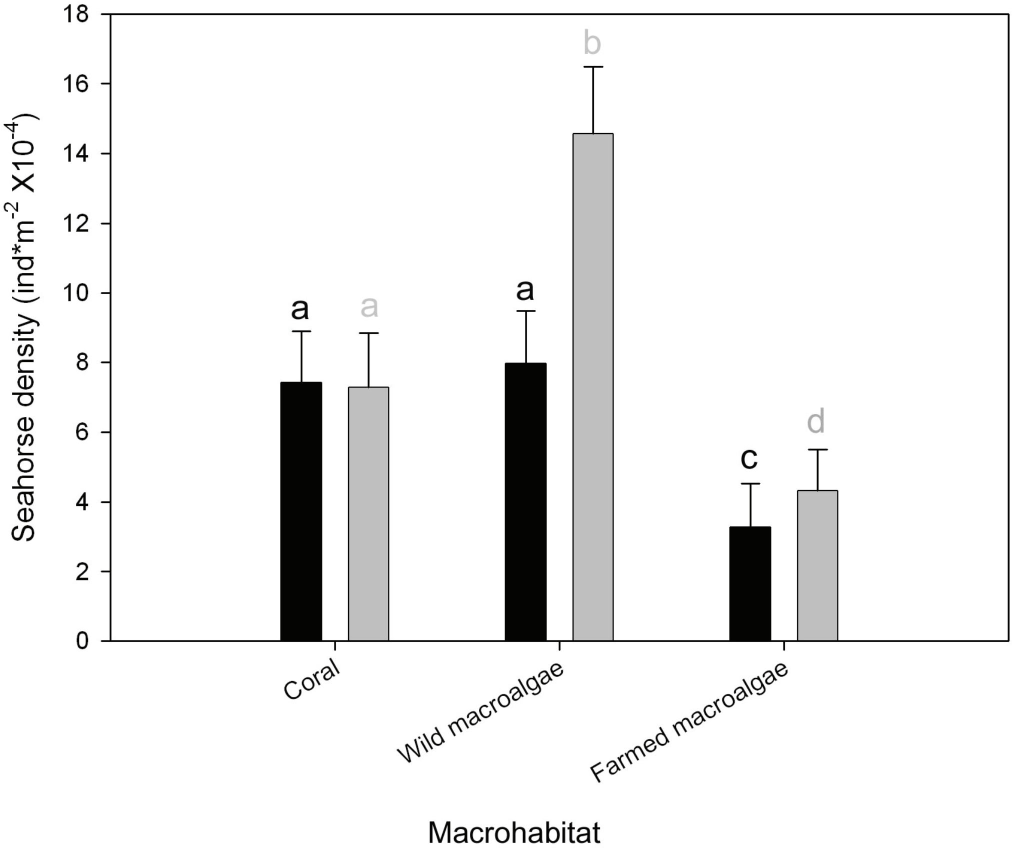

Figure 3. Mean + SE of adult (black) and juvenile (gray) density by reef zone for all surveyed transects on coral reef (n = 120 transects), wild macroalgae (n = 118) and farmed macroalgae (n = 81). Significantly different densities ($p<0.05$) (multiple comparisons) are given by different lower case letters.

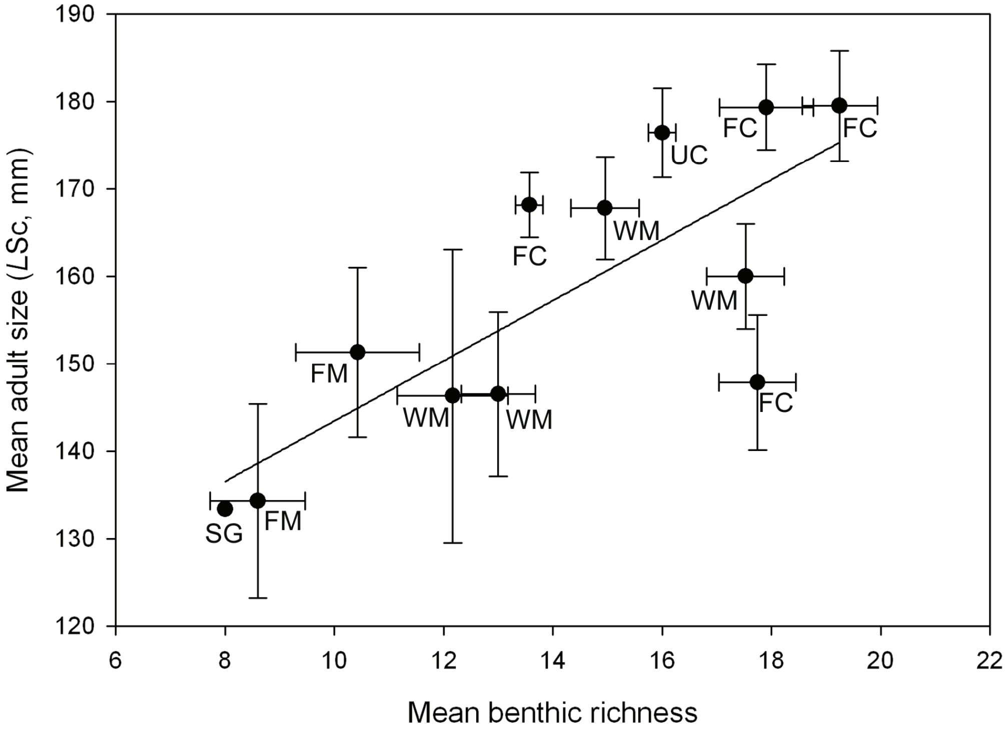

Figure 4. The positive correlation between benthic richness and mean adult size for all community-island combinations (Pearson product-moment correlation, r = 0.78). Values are means ± SE for benthic richness and adult size. FC, fished coral reef; FM, farmed macroalgae; SG, seagrass; UC, unfished coral reef; WM, wild macroalgae.

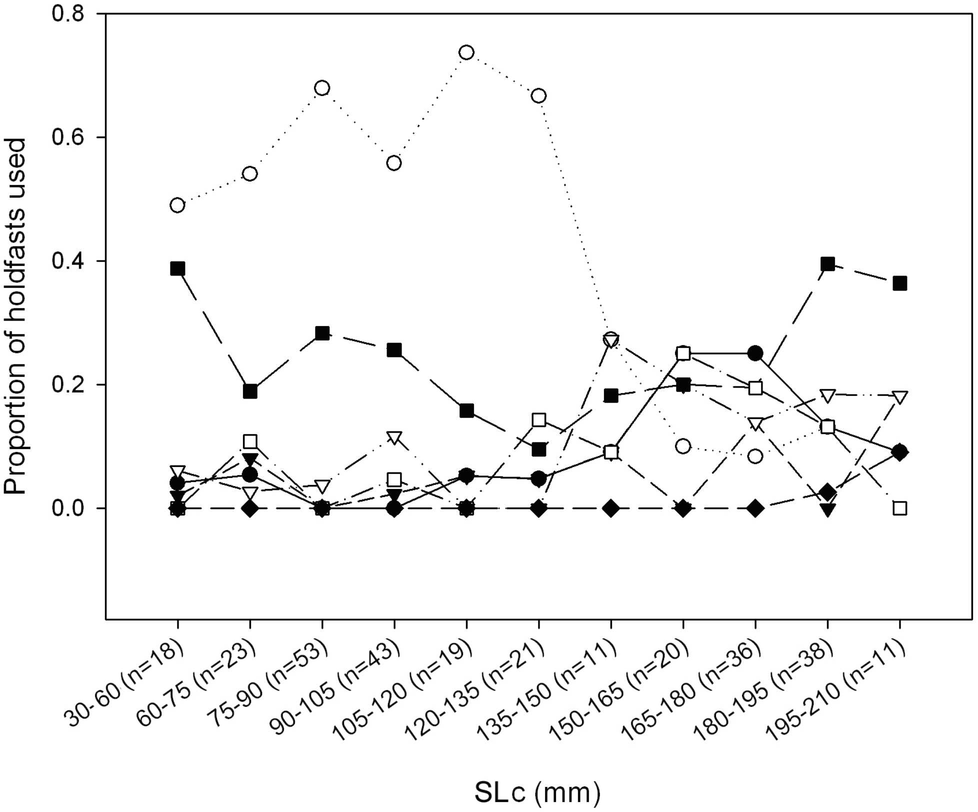

Figure 5. *Hippocampus comes* use of benthic substrata by size class (curved standard length, SLc) [(◊), abiotic structure; (◆), artificial structure; (●), coral; (○), macroalgae; (▼), other; (□), seagrass; (■), sponges].

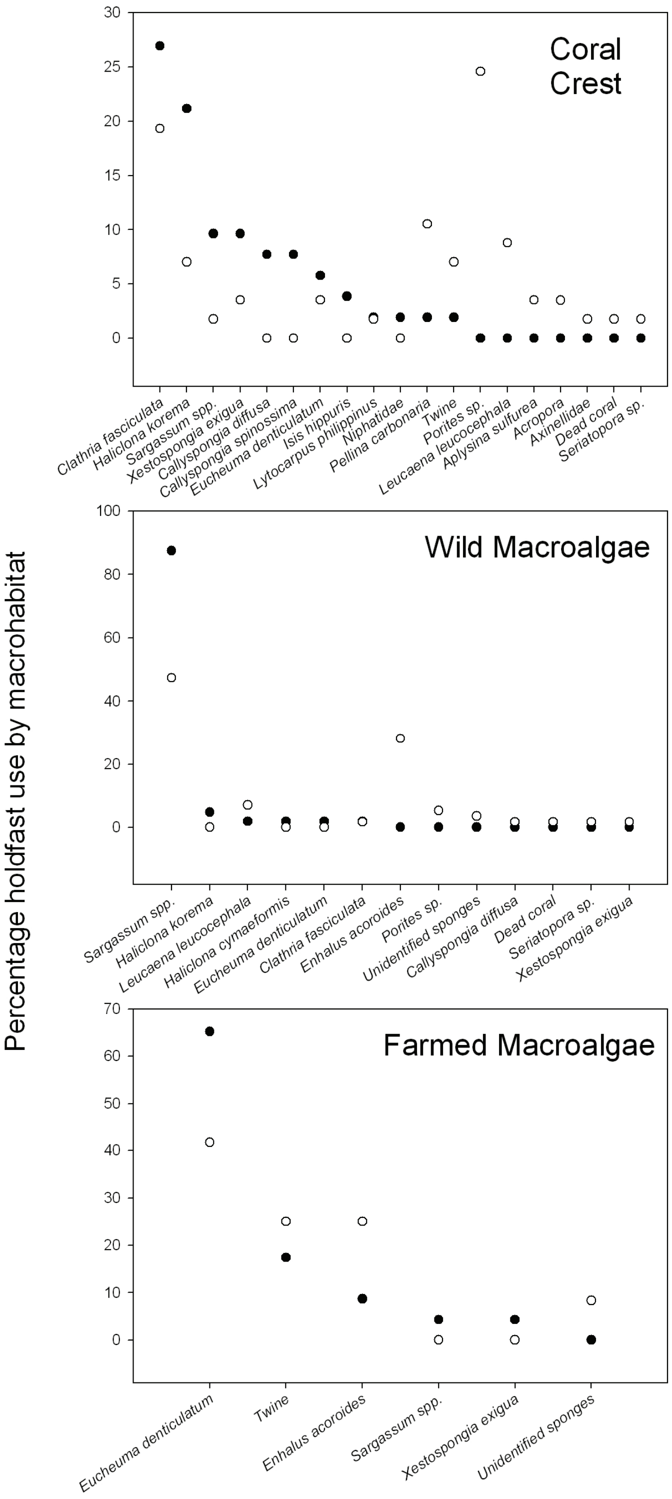

Figure 6. Holdfast use by juvenile (●) and adult (○) *Hippocampus comes* by reef zone, in: (a) coral reef, (b) wild marcoalgal beds and (c) farmed macroalgal beds.

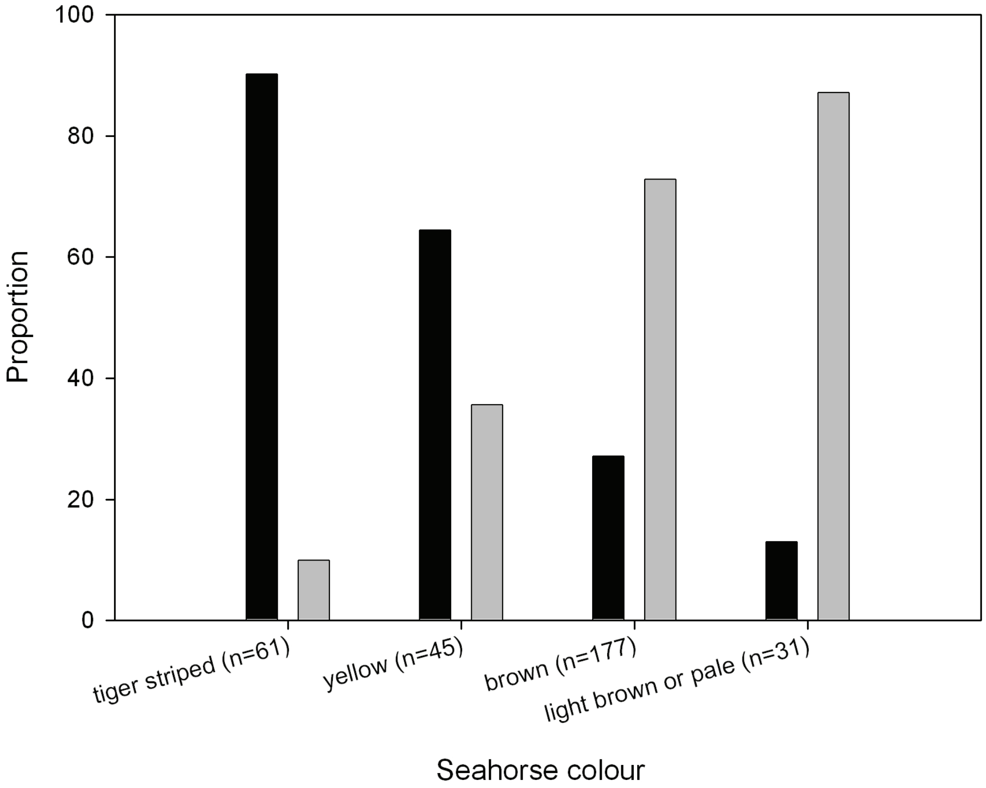

Figure 7. *Hippocampus comes* colouration as a function of life history stage. Black bars represent adults, gray bars represent juveniles.

LINKING STATEMENT IV

In Chapter 3, I showed that benthic size classes of *Hippocampus comes* exhibit ontogenetic shifts in habitat associations. Settled juveniles first used wild macroalgal beds as nurseries, grasping algae and sponges. Larger animals were found on reefs and used a greater diversity of holdfasts. These data are useful for future research and management of tropical seahorses, and point to the largely unexplored importance of wild macroalgal beds as nursery habitat for tropical reef fishes.

Where Chapters 1-3 focused on previously unknown aspects of the in situ ecology of sequential life stages, Chapter 4 consolidates and expands the scope of our understanding of demographic diversity in seahorses and provides the first quantification of vital rates for a tropical species in this mainly tropical genus. Information on growth, reproduction, and survival are necessary to predict how populations will respond to natural and anthropogenic perturbations. These will now be available to frame the life history of *H. comes* relative to other fishes, to act as reference points for other data-depauperate *Hippocampus* spp. and to model management options.

CHAPTER 4

LIFE HISTORY REFERENCE POINTS FOR MANAGEMENT OF AN EXPLOITED TROPICAL SEAHORSE

ABSTRACT

This research defined the life history and in situ vital rates of *Hippocampus comes* Cantor, 1850, a mid-sized tropical seahorse species from the central Philippines. We described the population structure, as well as growth, reproduction and survival rates of this heavily fished syngnathid. Our research drew on mark-recapture intervals from a focal observation grid, underwater visual census of fishing grounds and fisheries landings data. Assuming individually variable growth, we estimated the mean parameters for the Von Bertalanffy growth equation as Linf = 16.7 cm, K = 2.9 yr^{-1} and $t_o = 0.03$. *Hippocampus comes* reaches physical maturity at 9.3 cm (ca. 4.5 months), and becomes reproductively active at 11.6 cm (ca. 5.4 months). The central Philippines population exhibits a yearly recruitment pulse corresponding to the hot, dry, inter-monsoon window from February-May. At this time, first cohorts recruit to the benthos, usually at 3.0-4.0 cm, but at sizes as small as 2.7 cm. Survivorship varies with size, ranging from 3.5 % - 45.0 % yr^{-1} in settled juveniles versus large site-faithful adults. This species is estimated to live at least 2.5 years and perhaps longer. *Hippocampus comes* is small-bodied, grows quickly, matures early and reproduces repeatedly throughout the year, so shares many traits with opportunistic life history strategists. However, other reproductive characteristics of *H. comes,* such as large oocytes and extended parental care represent traits of equilibrium strategists. Marine protected areas are one management tool that may provide appropriate protection for this heavily fished species, particularly since currently adopted size limits will not protect important, large, fecund adults.

INTRODUCTION

The demographic characteristics of a species are one key factor that determines how its populations respond to natural and anthropogenic change. These rates form the basis of population models and fisheries reference points, and are necessary for management (King & McFarlane 2003; Winemiller 2005). Practical conservation initiatives including recovery programs and captive breeding also rely on knowledge of species' demography. Even partial demographic information for data-depauperate species is useful, given that life history traits from better-researched taxa can be used to provide inter- or intraspecific information about characteristics that are difficult to measure (Froese & Binohlan 2000; Pauly 1980). Linkages among life history traits also mean that demographic parameters can be used to generate useful a priori knowledge of factors such as species' roles in ecosystems (Shuter et al. 2005), susceptibility to risk (Jennings et al. 1999), and invasive capacity (Chizinski et al. 2006; Olden et al. 2006). Despite this, species' vital rates are usually unstudied or poorly understood prior to exploitation.

Demographic data are particularly needed for overexploited tropical reef fishes (Winemiller 1989) which are important both as key components of marine ecosystems and as vital resources for people. While official records estimate that reef fisheries comprise up to 10 % of the world catch, these numbers are likely to grossly underestimate their true value (Sadovy 2005). Reef fisheries are culturally significant , providing not only employment and income, but also 30-75 % of basic protein needs in some regions (Pauly 2006; Ratner 2006; Stobutzki et al. 2006b). However, Asian areas in particular, have experienced prominent recent declines in the biomass of demersal fishes, ranging from 36-90 % of baseline values (Stobutzki et al. 2006a). It is presently estimated that total landings from reef fisheries are 64 % higher than can be sustained and pressure on these resources is expected to increase (Newton et al. 2007). Relative to developed countries, resources for fisheries science in tropical, developing countries tend to be scarce. Furthermore, reef fisheries - in areas of high biodiversity where species tend to have smaller ranges than at higher latitudes (Stevens 1992) - are often multispecific, further complicating their assessment.

Seahorses (genus *Hippocampus*) are an example of a heavily exploited group of fishes where capacity for management is hindered by a rudimentary understanding of species' demography. Many of the 34 seahorse species found globally are fished and sold as cash commodities for traditional medicines, curiosities and aquarium display, rather than used for food (Vincent 1996). Precautionary management was implemented in 2004 to halt indiscriminate capture, believed to exceed 20 million animals per year (Giles et al. 2005; Vincent 1996). Seahorses are now listed as a genus on CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) Appendix II, which legally requires 172 signatory countries to ensure that their exports are documented and not detrimental to wild populations. The CITES Animals Committee has recommended that trading parties consider the use of a simple 10 cm minimum size limit, in the absence of other ways to assure the sustainability of exports (Notification 2004/033) (Foster & Vincent 2005). Now that first steps have been taken, adaptive management using robust demographic data is needed to refine this interim size limit and to model species-specific alternate policy options so that national fisheries can meet their commitments to sustainable use under CITES. Life history data are particularly needed for tropical seahorses, which make up 70 % of the genus *Hippocampus*. All species in the main medicinal trade presently have either partially or fully tropical distributions.

We here quantify population structure and key vital rates for the tiger tail seahorse, *Hippocampus comes* Cantor, 1850*,* in order to improve capacity for management and allow modelling of future policy options. This species has been fished in the central Philippines since the early 1960s and been studied since the mid 1990s. More information on population trends and demography has been collected for this species than for most other seahorses. Research has been conducted on this species' ecology and habitat use (Marcus et al. 2007; Morgan & Vincent 2007), genetic population structure (Casey 1999), market demographics (Pajaro et al. 1997, Project Seahorse, unpublished data), fishing patterns (Vincent et al. 2007) management (Martin-Smith et al. 2004) and trade (Vincent 1996). We now aim to a) generate a growth model from which to infer ages at ecologically relevant lengths, b) quantify reproduction and seasonal effects on reproduction, c) clarify natural and anthropogenic mortality, and d) compare these variables to those of other fishes in a management context. This research is based principally on novel data and also contains original analysis of data used in other research (Martin-Smith et al. 2004; Meeuwig 2001; Perante et al. 1998).

METHODS

Study System

Research was conducted from April 2001 to June 2003 on the Danajon Bank, a double barrier reef system that runs parallel to the northern and western coasts of Bohol province for ca. 145 km, in the central Philippines (Pichon 1977) (Fig. 1). The area is characterised by extensive seagrass beds and island-fringing mangrove communities and also supports a mixture of coral shoals, silt/sand flats and macroalgal beds. Waters in the regions have mixed semi-diurnal tides, moderate turbidity (0.5-4 m horizontal visibility) and annual temperatures that range between 25-32° C. The bank is heavily used by artisanal fishers, so reef platforms surrounding communities are subject to disturbance from boat hulls, anchors, trampling and destructive fishing methods. The central Philippines experiences two yearly typhoon seasons: from the southwest during June-August and from the northeast during September-January (Green et al. 2000; Wang & Ho 2002).

Study Species

Hippocampus comes is found only in the Indo-Pacific, and is believed to occur at greatest densities in the Philippines (Lourie et al. 2004). Populations have also been found in Indonesia, Malaysia, Singapore, Thailand and Vietnam (Lourie et al. 2004). *Hippocampus comes* inhabits coral reef, algal beds, and occasionally seagrass beds, at depths normally ranging from 0.5-10 m. Juveniles are most common in wild macroalgal stands, while adults predominate in crest reef habitat (Morgan & Vincent 2007). *Hippocampus comes* are patchily distributed and pairs can exhibit prolonged monogamy: recorded periods span up to 21 months (Perante et al. 2002). On the Danajon Bank, the seahorse fishery is very largely comprised (93 %) of *H. comes* (Pajaro et al. 2001), contributing to their status of Vulnerable (IUCN 2007). Previous genetic analysis indicates that individuals from the part of the Danajon Bank used in this study are likely to be part of a single interbreeding population (Casey 1999).

Measurements

Approaches to assessing size, sex and reproductive status used for most teleosts have to be adjusted for seahorses. The unusual shape of seahorses means that length is a composite of three partial body lengths; head length (HL), trunk length (TrL) and tail length (TaL). In this study, all measurements are standardized to straight standard length (SLs) (Lourie 2003) unless otherwise stated. Male seahorses possess a mature brood pouch and females sometimes exhibit a ventral egg bulge or distended ovipositors (Foster & Vincent 2004a). Where maturity was ambiguous, we retroactively assigned animals to juvenile or adult categories based on a cut-off of 10.5 cm, equivalent to the smallest males bearing young (L. Brady, unpublished data; Project Seahorse, unpublished data). Males were assigned a reproductive status (RS) of 0 (mature but empty), 1 (pregnant), 2 (ready to release young) or 3 (newly empty). Females were assigned to a RS of 0 (no evidence of eggs), 1 (may have eggs) or 2 (ready to transfer eggs) (Perante et al. 2002).

Data sets

Demographic information came from three main sources, as well as a suite of smaller data sets including dissections, aquarium studies and field observations. *First*, capture-recapture values were generated from tagged animals monitored on a focal observation grid at Cataban Island, on Danajon Bank. *Second*, seahorse size and abundance were estimated using underwater visual censuses (UVC) on belt transects across representative habitats in the Danajon Bank. *Third*, we obtained morphometric and reproductive information from *H. comes* landed from 1996-1998 and 2002-2004 in the seahorse fishery at Jandayan Island, Danajon Bank (Vincent et al. 2007). We also accessed information on dissections from 95 % EtOH-preserved pregnant males (n = 108), captured in the Danajon Bank fishery (L. Brady, unpublished data).

(1) Capture Mark Recapture (CMR), Focal Observation Grid

Data on abundance, growth and survivorship were collected from April 2001-May 2002 via mark-recapture on a 2880 m^2 area of subtidal shallow reef, in Cataban Island's marine reserve (10°13.75'N, 124° 23.36'E) (Fig. 1). This focal observation area was chosen for its no-take status, the known presence of seahorses and an abundance of potentially suitable habitat (Perante et al. 2002). We built a grid measuring 2400 m^2, with two 240 m^2 eastern and western buffer zones, that was divided into 2 m X 2 m squares. Animals were initially located with the help of seahorse fishers during a two week search period in early April 2001 and thereafter given adjustable numbered collar tags (Morgan & Martin-Smith 2004) or permanent marks with visible implant fluorescent elastomer (VIFE), an injectible plastic polymer that has no, or minimal (ca. 1 %) non-lethal effects, on the condition of seahorses (Curtis 2006; Woods & Martin-Smith 2004).

From 15 April 2001- 14 May 2002, we conducted regular UVC (n = 102 partial or full surveys) on the focal grid. Upon initial capture, morphometrics were measured using vernier calipers. On census dives, for every seahorse, we recorded sex, reproductive status, depth, holdfast type, seahorses' height on holdfasts, holdfast size and time of sighting.

(2) Underwater Visual Census (UVC), Stratified Habitat Surveys

Seahorse abundance and size was surveyed monthly from Feburary to April 2003 at four islands in the Danajon Bank: Cataban, Saag, Sagasa and Mahanay (Fig. 1). At each island, we examined four habitat strata (sites): coral reef, wild macroalgal beds, farmed macroalgal beds and seagrass meadows. Up to ten 600 m^2 (as area allowed) belt transects were laid haphazardly parallel to depth contours at each site (Morgan & Vincent 2007). Then two experienced seahorse fishers visually surveyed transects for seahorses after dark, when animals rise up on holdfasts and are most visible. A total of 393 transects and 230 173 m^2 were censused for seahorses over a period of 49 nights. We recorded the same data for each seahorse as in the CMR.

(3) Fisheries Landings

From 1996-1998 and 2002-2004, colleagues on our team recorded the morphometry, sex and reproductive status of seahorses landed by artisanal lantern fishers in Handumon village, Jandayan Island, Bohol (Fig. 1) (Vincent et al. 2007). Animals were measured either alive or <6 hours after capture, using vernier calipers. We analyzed only those individuals for which complete length measurements were available (HL + TrL + TaL) and that did not have clipped tails. Catch numbers were converted to proportions for analyses where the relative abundance of animals at a given size was important.

Data Analysis

Growth

Relationships between standard length and body morphometry were calculated based on fisheries landings (n = 6382) and data from L. Brady (n = 108). Abundance varied by size class, so we randomly sampled landings data to obtain the lengths of no more than n = 100 individuals per 10 cm size class (some contained fewer) to build unbiased regression relationships between partial body measurements and standard length, for males (n = 994), females (n = 1044) and juveniles (n = 98).

Estimates of growth parameters for *H. comes* were made assuming that this species, like most fishes, exhibits Von Bertalanffy growth (Curtis & Vincent 2006):

$$L_t = L\inf{}^*(1-e^{-K(t-to)}) \qquad \text{(Eq. 1)}$$

where Linf is mean asymptotic length (cm), K is the metabolic growth coefficient (years^{-1}) and to is a theoretical age t, at which the length is 0 cm.

To estimate growth we used a method that assumed that individual seahorses in the Danajon Bank population grew to variable final lengths following unique, individual Von Bertalanffy growth functions (VBGF). Individual variation in fishes is ubiquitous (Wang 1998) and we found evidence that individual seahorses of similar lengths exhibited variable growth, since animals on our focal grid were showing asymptotic growth at lengths substantially less than the largest individuals from fisheries landings.

We drew on five sources of data: two sets of mark recapture intervals from in situ populations of adults within protected areas on the Danajon Bank (n = 44 intervals, focal observation grid; n = 155 intervals, Project Seahorse unpublished data), two sets of intervals generated from juveniles of known age reared in aquarium facilities (n = 30 intervals, S.K. Truong, unpublished data.; n = 32 intervals, Job et al. 2006), and intervals from monthly modal progression of unfished juvenile size classes from underwater visual censuses on the Danajon Bank (n = 2, iterated X 16). The latter were iterated to give these data comparable weight to other juvenile data sets used in maximum likelihood methods described below. By using nearly twice the number of intervals from mature versus immature individuals, we placed greater importance on growth of individuals above maturity, known to conform strongly to Von Bertalanffy growth (Lester et al. 2004).

To make maximum likelihood estimates of K and the mean and variance of Linf (Linf$_m$ and Linf$_{var}$, respectively) we employed the methods of Wang et al., (1995). This approach involves a direct, one-dimensional search of the value for K that maximizes the likelihood of the observed lengths of recaptured individuals, and which also yields estimates for Linf$_m$ and Linf$_{var}$. We assumed that K for the population was a constant (as per Wang & Thomas 1995), and that measurement error was negligible relative to the multi-month duration of recapture intervals.

We also verified via Lilliefor's tests that the Linf and T values calculated from recaptured individuals were lognormally distributed, using estimates for these parameters calculated from initial (L_M) and recapture (L_R) lengths taken T fraction of a year apart:

$$L\inf = L_R + \frac{e^{-Kt}}{1-e^{-K_{est}t}}(L_R - L_M) \qquad \text{(Eq. 2)}$$

$$T = \frac{-1}{K_{est}}\log\left[1-\frac{L_M}{L\inf}\right] \qquad \text{(Eq. 3)}$$

where an initial estimate of K$_{est}$ was used to set Linf and T values for each individual. Here, initial K$_{est}$ was set at 2.2, calculated using Faben's method (Fabens 1965). Linf and T values were then used to calculate the mean and variance of each distribution, which were in turn used iteratively to estimate the likelihood of each L_M and L_R pair, given the initial K$_{est}$ value:

$$Lik(L_M, L_R|K) = \frac{\Pr(T) * \Pr(L_{\inf})}{(L_R - L_M * e^{-Kt})(Ke^{-KT})} \qquad \text{(Eq. 4)}$$

where Pr(T) and Pr(Linf) are the probabilities of these estimates, assuming lognormal distributions and the moments estimated as described above. The negative log-likelihoods are then summed across individuals to yield a total negative log-likelihood, which is minimized:

$$-\log Lik_{Total} = \prod_i^N -\log\left(Lik(L_M, L_R \mid K\right) \qquad \text{(Eq. 5)}$$

The Matlab program and data used to execute this method are found in Appendix I. Using the final most likely growth coefficient (K = 2.9), we then calculated the mean population Linf and its variance (σ). Uncertainty around Linf was quantified by generating pseudo 95 % confidence intervals using the program in Appendix II.

The last model parameter, theoretical age at which length was 0 cm, t_o, was estimated by knowledge of length at recruitment (Lr) and age at recruitment (tr) via the relationship t_o = tr+1/K(ln(Linf-Lr/Linf)) (Ricker 1975). Length at recruitment was set at the 0.35 cm midpoint of the first recruited cohort which ranged from 0.30-0.40 cm in underwater visual censuses. These individuals were estimated to be 10 days old based on growth rates from young reared ex situ (Job et al. 2006). Growth rates from other species of aquarium-reared seahorses approximate rates seen in wild populations (Curtis & Vincent, 2006).

Reproduction

(1) Spawning, Recruitment and Reproductive Seasonality

The spawning season was estimated using the Von Bertalanffy growth equation (Eq. 1), parameterized for *H. comes* (Eq. 6), to back-calculate the date of release (seahorse young are brooded by male parents) for all landed individuals based on their size on a given capture date. Spawning was then graphed as the monthly percentage of births over the year. Recruitment was plotted as the percentage of landings that was juvenile by month, corroborated by underwater visual census of n = 393 benthic transects in habitat representative of the Danajon Bank (Morgan & Vincent, 2007). We followed conventions of reef fish ecology in defining recruitment as "an estimate, subject to variation in methodology and artifacts, of the real biological phenomenon of settlement" (Hixon & Webster 2002).

Seasonal effects on reproduction were also examined by analyzing whether a) reproductive duration (time spent brooding per male), and b) the proportion of males pregnant, changed by month. Reproductive duration was measured as the time in days between two consecutive RS 3 events in males. We considered only cycles <30 days in duration, based on previous estimates of reproductive cycles ranging from 14-21 days (Martin-Smith et al. 2004). In some cases, RS 3 events were predicted based on observed RS 2 animals, where the RS 2 stage was assumed to last an average of 5 days, because 27 % of the male population exhibited RS 2 status at any given time (0.27 X 17.5 day cycle = 4.7 days) (Fig. 2). Insufficient monthly data were available to analyse whether the proportion of males pregnant varied seasonally.

(2) Maturity and Reproduction

Using logistic regression, we plotted the proportion of individuals in a given reproductive stage against standard length and took the 50 % transition point as the size at which this attribute appears in the population. Sizes were binned in 10 cm intervals. To determine length at physical maturity, Lm, we identified the size at which 50 % of males had mature brood pouches and females were mature. Similarly, to determine length at reproductive activity, Lr, we calculated the proportion of adults pregnant or with eggs (RS 1, 2) versus all individuals of that size. We also estimated the size at spawning, Ls, as the proportion of females about to pass hydrated eggs or males about to release young (RS 2), relative to same-length individuals in the population.

(3) Fecundity

Relationships between length/mass and brood size were generated by haphazardly selecting males for dissection from fished catch that spanned the full size range of mature individuals seen in the fishery (L. Brady, unpublished data). Since other seahorses have shown reliable relationships between length/mass and brood size (Texeira & Musick 2001; Woods 2005) and because *H. comes* is known to release broods over multiple nights (S. Morgan, pers. obs, J. Anticamara, pers. comm.), we inferred that the lower mode in embryo number represented partial releases.

Survival and Longevity

Survivorship or its inverse, mortality, was calculated three different ways following Curtis & Vincent (2006): using capture mark recapture (CMR) information, via empirical relationships and using a length-converted catch curve created from landings data.

(1) CMR

Using CMR data from our focal grid, we generated estimates of apparent survival, Φ, and probability of recapture, p, via Program MARK™ 4.3. We used Cormack Jolly Seber (CJS) models because data were collected from an open population of live animals that were visually recaptured then "released" alive on successive occasions (Krebs 1989; White & Burnham 1999). A total of 93 survey nights from April 2001–April 2002 were agglomerated into 68 observation periods, which each represented one full examination of the focal grid: no observation periods exceeded a total of 14 days. Re-sightings (1s) and absences

(0s) were used to create numerical sequences describing encounter histories for each individual on the focal grid.

Before modelling, we used goodness of fit tests (GOF) from program U-CARE to check that the structure of data in our most parameterized starting models [$\Phi(t*s)p(t*s)$] and [$\Phi(t*l)p(t*l)$] met the assumptions underlying the chosen CJS model, particularly that every marked animal at time (i) had the same probability of recapture (pi), and had the same probability of surviving to time (i+1). GOF tests from program U-CARE are most appropriate when working with sparse cohort-specific contingency tables that arise when new animals are found infrequently, as we saw on the focal grid.

Sex (s), length (l) and time-specific (t) differences in apparent survival and recapture probabilities were investigated among two sets of sixteen candidate models that examined combinations of time-invariant [$\Phi(.)p(.)$], time-variant [$\Phi(t)p(t)$], or sex/length-specific [$\Phi(s/l)p(s/l)$] apparent survival and recapture probabilities. To examine length-based differences in Φ, animals were divided into biologically relevant size classes corresponding to juveniles (immature, <9.6 cm), small adults (mature, 9.6 - 17.0 cm) and large, site faithful adults (mature, > 17.0 cm). Models were compared on the basis of the Quasi likelihood adjusted Akaike Information Criteria (QAICc), and selected using rules of thumb given in Cooch & White (2004), which advise that models are well differentiated at QAICc values >7, but not at values <2.

(2) Empirical Equations

Natural mortality, M, was also estimated using the empirical "Pauly equation" (Pauly 1980): $\log_{10}M = -0.0066-0.279 \log_{10}Linf+0.6543\log_{10}K + 0.463\log_{10}T$, where Linf (cm) and K ($year^{-1}$) are parameters from the Von Bertalanffy growth equation and T (°C) is the mean annual water temperature, which we calculated over the study period to be 28.5° C (S.K.M., unpublished data). Annual survival rate, S, was calculated from natural mortality, M, via the equation, $S = e^{-M}$, expressed as a percentage (King 1995).

(3) Catch Curve

Last, we used length-converted catch curves to estimate total mortality, Z (Pauly 1990). Since total mortality is composed of both natural, M, and fishing mortality, F, we used estimates of M from Program MARK to estimate F via the relationship $Z = M+F$. F and Z were converted to S as above.

Absolute longevity, t_{abs}, was estimated in situ based on the three longest re-sighted individuals in protected populations, inferring time prior to first sighting based on the VBGF in Eq. 6. We also projected mean lifespan, t_{max}, using the meta-relationships $t_{max} = 3*K^{-1}$ (Pauly 1980) and $\mathrm{Log10}(t_{max}) = 0.5496+0.957*\mathrm{Log10}(tm)$ (Froese & Binohlan 2000).

RESULTS

Growth

We used mark recapture/growth intervals and maximum likelihood methods that estimated a probable K value of 2.9 yr^{-1}. Using this value, we estimated mean population Linf at 16.7 cm, and then t_o at 0.03, giving a Von Bertalanffy growth function (Eq. 1) for *H. comes* in the Danajon Bank as:

$$L_{t\,H.comes} = 16.7\left[1 - e^{-2.9(t-0.03)}\right] \qquad \text{(Eq. 6)}$$

Confidence intervals (CI, 95 %) around mean Linf reflected individual variation in growth, placing Linf between 8.94 cm (lower CI) and 28.5 cm (upper CI). Length-length equations for converting between partial body measurements and different forms of full size are given in Table 1.

Reproduction

Spawning, Recruitment and Reproductive Seasonality

Hippocampus comes is reproductively active throughout the year (Fig. 3, 4A), but also exhibits an annual recruitment pulse that was clearly visible in UVC (Fig 4B). The same recruitment pulse was visible in landings and begins in January, peaks in February and March, then wanes after May (Fig. 4B). During this period, the proportion of juveniles in fisheries landings increases from <5 % to ca. 40 % of catch (Fig. 4B) and small cohorts begin to appear in UVC at 3.0 cm SLs (Fig. 3). From this recruitment pulse, we used growth rates to calculate potential reproductive output earlier in the year. By inference, reproduction (successful output of young) peaked in October at 13 %, and decreased to a low of only 5 % of annual spawning in February and March. The duration of reproductive cycles changed by season, with brooding intervals ranging from a mean (± SE) low of 13.4 ± 0.82 days from March–August, and increasing to an average of 20.2 ± 0.31 days during colder weather from September-February (Fig. 4C).

Maturity and Reproduction

In both sexes of *H. comes,* young reach physiological maturity well before they engage in reproductive activity (Fig. 2A, 2B). Mean male maturity, Lm_{male} ± SE, corresponded to 93.1 ± 0.6 mm SLs (logistic regression, proportion mature = 1.0051 / (1+exp-((SLs (mm)-93.1)/6.2)), n = 18, p<0.001). Onset of reproductive activity occurred when individuals were 23 mm larger than Lm_{male}. Whether defined by the size at which males were pregnant, Lr_{male}, or about to release young, $Ls_{male,}$ half of males in the population were brooding at 116.3 mm ± 6.4 mm (logistic regression, proportion reproducing = 0.6835 / (1+exp-((SLs (mm)-116.3) / 17.2)), n =16, p<0.001)(logistic regression, proportion releasing = (0.2610 / (1+exp-((SLs (mm)-116.4) / 5.50)), n = 16, p<0.001).

Maturation and reproduction apparently occurred at smaller sizes in female than male *H. comes*. Females seemed to reach physical maturity, Lm_{female}, at 79.4 ± 1.3 mm (logistic regression, proportion mature = 0.9959 / 1+exp-((SLs (mm)-79.4) / 7.65), n = 16, $p<0.001$), and become reproductively active at sizes larger than Lr_{female} = 85.2 ± 3.4 mm (logistic regression, proportion reproducing = 0.6425 / (1+exp-((SLs (mm)-85.2) / 8.00), n = 16, $p<0.001$) (Fig. 2B).

Since maturity and reproductive status are challenging to identify in females, and because females may produce eggs before engaging in regular mating activity, we used Lm_{male} and Lr_{male} to generate age at maturity, tm = 3.8 months, and age at reproduction activity, tr = 5.4 months, for the species.

Fecundity

Fecundity increases linearly as a function of body size. Over a broad size range of reproductive males (n = 31) (Fig. 5A), there was a bimodal distribution in embryo number (Fig. 5B). Since the lower mode probably represented partial broods (see methods), we generated relationships between two independent size metrics for fathers – (a) SLs and (b) mass after embryo removal – and the upper mode of embryo frequency. Both measures showed similar, significant, but weakly positive relationships with brood size (embryo number = -2.69+3.14*SLs (mm), n = 18, $R^2 = 0.24$, p = 0.03) (embryo number = 307+26.8*Mass (g)), n = 18, $R^2 = 0.31$, p = 0.01) (Fig. 5C, 5D).

Survival and Longevity

Goodness of fit tests run before model-fitting showed that the data conformed to assumptions of the open CJS model (Global Test, groups = 2, df = 196, quadratic $X^2 = 181.9$, p = 0.76). There was no evidence for transience (directional mobility) (Test 3SR: N (0,1) 2-sided signed statistic = 0.37, p = 0.71), but there was a significant effect of trap dependence (Test2CT: N(0,1) signed test statistic = -9.35, $p < 0.001$), indicating that some *H. comes* were more likely to be re-sighted again once sighted initially.

The best fit of our CMR data via an open CJS model indicated that survivorship was independent of time and sex, while recapture rate was affected by sex [Φ(.)p(s)] ($QAIC_{\Phi(.)p(s)} = 1604.6$, deviance = 1545.93, 3 parameters (Φ, p_f,p_m)). A second model [Φ(s)p(s)] was not significantly different from the best fit model ($QAIC_{\Phi(.)p(g)} = 1604.6$, deviance = 1545.93, 3 parameters (Φ, p_f,p_m) vs. $QAIC_{\Phi(g)p(g)} = 1606.6$, deviance = 1545.90, 4 parameters (Φ_f, Φ_m, p_f, p_m)) and suggested that there may be a minor effect of sex on survivorship with females surviving marginally more often ($\Phi_f = 0.9952 \pm 0.001$, $\Phi_m = 0.9949 \pm 0.001$). These daily survivorship rates correspond to annual survivorship of 17.52 % in females ($M_{female} = 1.856$ yr^{-1}) and 15.63 % in males ($M_{male} = 1.742$ yr^{-1}). Males were more frequently re-sighted than females ($p_m = 0.79 \pm 0.02$, $p_f = 0.69 \pm 0.02$).

A second series of Mark models that tested the effect of size and time on survivorship indicated that both recapture and survival rates were influenced by size. Juveniles (<9.3 cm) and small adults (9.3-17.0 cm) showed similar re-sightability ($p_{juv} = 0.69 \pm 0.08$, $p_{sa} = 0.68 \pm 0.02$), although confidence intervals were broader around juveniles ($CI_{juv} = 0.51$-0.82 vs $CI_{sa} = 0.64$-0.72). Large adults (>17.0 cm) were significantly more often re-sighted ($p_{la} = 0.78 \pm 0.2$, $CI_{la} = 0.75$-0.81). Survival of juveniles, small adults and large site faithful adults was 3.5 %, 10.4 % and 45.3 % annually respectively. Survival estimated from Pauly's method (Pauly 1980) were low (1.48 % annually) and corresponded poorly with estimates of even the youngest size classes from program Mark.

On the Danajon Bank, fishers begin targeted extraction of animals at ca. 7.0 cm, 2.0 cm below physical maturity, with full exploitation occurring above 15.0 cm SLs (Fig. 6). Catch curves from seahorse landings estimated total mortality of *H. comes* outside the marine reserve, in grounds frequented by lantern fishers at $Z = 4.36\ yr^{-1}$.(linear regression, $y = 13.06-4.36x$, $df = 7$, $p <0.0001$) (Fig. 6). Subtracting mean overall natural mortality in males and females ($M_{overall} = 1.79\ yr^{-1}$) from total mortality gave an instantaneous fishing mortality rate of $F = 2.57\ yr^{-1}$, and an exploitation ratio, F/Z, of 0.58 for sexually mature adults. Fishing mortality will be even higher for the largest and fully exploited individuals (>170 mm), where $F = 3.57\ yr^{-1}$ and $F/Z = 0.82$.

We estimate that *H. comes* is likely to live at least 2.5 years in the wild and possibly longer. Using Eq. 6 to age the longest observed individual from CMR, then adding 21 months of observation, we estimated longevity at 33 months or 2.7 years: at least two other individuals also attained estimated ages of 2.4 years. It is possible that *H. comes* may live over 3 years. Three individuals on the focal grid were captured at initial lengths of 17.0-18.4 cm, and were present 13 months later. It was not meaningful to assign an initial age to these individuals who were above mean asymptotic length in our VBGF. Using Lr_{male}, mean longevity was estimated to be 2.0 years, with the standard error (SE) of the range from 1.3-3.1 years (Froese & Binohlan 2000), while estimates from the Pauly method (1980), predicted only a 1.0 year lifespan.

DISCUSSION

The vital rates presented here for *H. comes* represent the most comprehensive in situ demographic information presently available for a tropical seahorse from this primarily tropical genus. Focusing research on a single warm-water seahorse species may be the most efficient means of generating a clear understanding of this taxon, in reef ecosystems with limited resources for management. Analyses show that this small species grows rapidly, matures young, reproduces frequently throughout the year and is probably short-lived. Comparable vital rates are shared by other tropical syngnathids. Most of the rates that govern population turnover in *H. comes* confer low susceptibility to risk (Roberts & Hawkins 1999), but their brooding parental care and monogamous mating increase risk under exploitation. Together, these traits confer a life history intermediate between opportunistic and equilibrium strategies. Explicit modelling of management scenarios, using best available demographic information, will help to suggest best policy options.

Growth

Hippocampus comes grow rapidly at rates that are comparable to other syngnathids. Seahorses and pipefish from warm waters exhibit K values that range from 0.34 -2.80 (Table 2). Like most fishes, growth rates in tropical species exceed those of temperate species (Pauly 1998). Growth coefficients for this study and observed in other tropical syngnathids are high, but within ranges typical for reef fishes in tropical regions (Fig. 7), and may be inflated in studies that have focused on juveniles (Choo & Liew 2006; Job et al. 2006; Job et al. 2002; Santos 2000; Takahashi et al. 2003; Wilson & Vincent 1998) (Table 2).

Our research predicted lower Linf values and higher growth coefficients than other studies on *H. comes* (Table 3). This is expected when other approaches (such as Faben's method) fix growth parameters and assume a single growth trajectory for all animals in a population (Wang et al. 1995). Previous estimates for growth parameters of *H. comes* were based on length frequency data (cf growth intervals were used here), and defined Linf from the largest individuals in the population, rather than by assuming (as we did here) that Linf is variable among eldest (but differently sized) individuals in the population. Previous work on *H. comes* may also have underestimated growth rates since data came from fisheries dependent landings of animals above ca. 7.0 cm that did not include rapidly growing juveniles (Meeuwig 2001).

Growth rates of *H. comes* derived from animals on the Danajon Bank may have been affected by fishing pressure, so could differ from the demography of this species elsewhere. Size-selective capture has cumulative effects on size at age

(Swain et al. 2007). When faster growing and large individuals are removed first, this downwardly biases estimates of mean asymptotic length (Linf), and upwardly biases estimates of K. In populations depressed by overfishing, growth rates may also increase through density-dependent effects (McGarvey et al. 1999). *Hippocampus comes* has been fished in the Danajon Bank since at least the 1960's (Perante et al. 2002), and fishing pressure is high with exploitation ratios >0.5. With the systematic removal of large individuals which command highest prices in the dried seahorse trade (Vincent 1996), growth rates may have increased, and asymptotic lengths decreased. Using growth parameters derived from the Danajon Bank could therefore underestimate Linf, overestimate growth rates, and predict greater resilience than may actually exist for unfished stocks of *H. comes* (or the converse for populations that are yet more heavily exploited).

Reproduction

Hippocampus comes reproduces year around and experiences a single annual recruitment pulse: highest densities of young are seen in "spring/summer", or the period when water temperatures increase following the coldest period of the year. Seasonal, summer-biased recruitment is common to syngnathids from both temperate and tropical regions (Table 2). In the Philippines, neritic fishes are thought to exhibit recruitment patterns that are related to the timing of monsoons. Most stocks (89 %, n = 112) possess two recruitment events, while fewer (11 %) show unimodal recruitment (Pauly & Navaluna 1983). In *H. comes*, recruitment appears to peak once, approximately three months after the height of the northeast monsoon, which occurs from November-January in Bohol Province.

Seasonal changes in recruitment may result from: (a) increased reproductive output, (b) increased planktonic survivorship, or (c) increased post-settlement survivorship. First, the abundance of young can increase with shorter reproductive duration (yielding more broods per unit time), greater brood size or greater proportion of reproductive animals in the population: all require further seasonal research. The abundance of reproductive males (and hence young) could also increase if fishers target species other than seahorses during certain times of the year (e.g. during the backalculated reproductive pulse in October). Second, planktonic survivorship may increase following upwelling effects induced by monsoons (the "Lasker-Bukun" hypothesis in Navaluna & Pauly 1984), or, recruitment may be more successful during calm inter-monsoon periods, where low wind activity minimizes loss of larvae to the open ocean (Johannes 1978). In Bohol, February to May corresponds to calm ocean conditions following the Northeast monsoon. Third, fluctuating biomass dynamics of wild macroalgal beds used by young may affect juvenile survivorship (Ang 1985; McCourt 1984; Trono & Lluisma 1990). It is also possible, but unlikely, that greater water visibility from February to May increases fishers' ability to find small animals, creating an apparent recruitment pulse where none exists (Perante et al. 1998). Newly settled juvenile cohorts appeared clearly in our UVC surveys (with smallest animals settling in February, when visibility was still poor) and experienced seahorse fishers who lantern-fish intermittently during periods of optimal conditions throughout the year, consistently identify February to May as the recruitment period for seahorses.

Size-assortative mating (Foster & Vincent 2004a) and personal experience suggest that apparent reproduction of females at sizes ca. 30 mm smaller than their male counterparts was caused by misidentification of juveniles without brood pouches, as mature females. This may also be responsible for the poor alignment between size at spawning, $Ls_{female} = 102.3 \pm 3.5$ mm, and size at reproduction, Lr_{female} (85.2 ± 3.4 mm), along with inaccurate differentiation between female reproductive stages (RS 0, 1, 2). Juvenile misidentification is visible as size distributions with prominent left tails spanning the smaller size classes in female reproductive stages, when compared with males (Fig. 2C).

The 1.5 month (2 cm) delay between physical maturity and the onset of reproduction is likely to be associated with finding a mate and establishing pair bonds. Reproductive behaviours associated with pairing seen in other seahorses (Foster & Vincent 2004a), that include complex courtship dances, rising in the water column to transfer eggs and changes of colour upon greeting (Vincent & Sadler 1995), are assumed to occur in *H. comes*, which are repeatedly found in the same pairs (Perante et al. 2002), but have yet to be documented in situ. *Hippocampus comes* does exhibit ontogenetic shifts in habitat use at approximately 13.5 cm, which is ca. 2.0 cm larger than Lr.

In *H. comes*, reproductive output increased positively with size such that large (and perhaps old) individuals make the greatest contributions to progeny comprising future generations. The positive relationship between length and brood size exists in many teleosts (Froese 2004) including other syngnathids (Strawn 1958; Texeira & Musick 2001; Woods 2005). The relative contribution of large adults may be even greater if young from these individuals grow quickly and experience enhanced survivorship: both have been noted (ex situ) in *H. kuda,* a sympatric congener of *H. comes* (Dzyuba et al. 2006). The potential importance of large, fecund adults should be recognized when exploring management alternatives for seahorses. Recommendations, such as minimum size limits (MSLs) that allow the removal of large, reproductive adults may jeopardize population-level reproductive output and cause selective evolutionary shifts in life history traits. MSLs are presently favoured by stakeholders (Foster & Vincent 2005; Swain et al. 2007) who prefer to catch the largest seahorses which command the greatest prices at market (Martin-Smith et al. 2004).

Survival and Longevity

Apparent survivorship from Mark (% S = 16.4 % annually) probably represents *H. comes* well, since a similar CMR study inside a second reserve on the Danajon Bank produced similar values (% S = 18.8 % annually) (Project Seahorse, unpublished data). Little is known about the causes of natural mortality in wild tropical seahorses, but we have observed depredation of artificially released *H .comes* young by large resident Pacific gregory damselfish, *Stegastes fasciolatus* (Chapter 1) and tropical seahorses have been found in the stomachs of tuna, rays, skates and dolphinfish (Alverson 1963; Herald 1949; Sharpe 1998; Wilson & Beckett 1970). Lethal pathogens have been identified in several *Hippocampus* spp. (Alcaide et al. 2001; Vincent & Clifton-Hadley 1989) and regularly cause mortalities in aquarium-held animals (Wolf 1998).

In the Danajon Bank, survivorship is heavily influenced by extraction, with fishing mortality representing >50 % of total mortality. The current exploitation ratio (0.58) indicates heavy fishing pressure and overcapacity among lantern fishers in the Danajon Bank, similar to fisheries elsewhere in the Philippines (Aripin & Showers 2000). Pressure is most intense on adults which command the highest prices in the dried trade (Vincent 1996). Large adults normally exhibit high survivorship, so that mortality imposed by extraction will be structured differently from natural mortality, which is highest in smaller size classes. Present exploitation practices risk both growth and recruitment overfishing. In the former, fish are taken at a rate that exceeds the optimal yield per recruit, so that more fishing yields less catch and hence fewer economic benefits than could be generated from a resource. The latter occurs when the number and size of adults being extracted decrease a population's reproductive potential to the point where it no longer has the capacity to replenish itself (Peterson 2002). Use of current CITES-recommended minimum size limits would do little to preclude recruitment overfishing. While comprehensive stock assessments for most tropical seahorse populations are not feasible, estimates of natural and fishing mortality can be used to establish appropriate fisheries reference points (Die & Caddy 1997). Even these methods make assumptions such as steady state dynamics that should be investigated by annual fisheries independent surveys.

Estimates of natural mortality and longevity based on empirical equations aligned poorly with our estimates, suggesting either that seahorses live longer than would be expected relative to other fishes, or that these relationships may not always represent taxa such as seahorses well (Foster & Vincent 2004a). For example, length-based empirical equations often assume a direct relationship between length and age that is not consistent with individually variable growth observed in *H. comes*. Similarly, recent research on tropical fishes (e.g. *Lutjanus* spp.) shows that size and age can be effectively decoupled, particularly in species with "square" growth curves, such as *H. comes*. Species with similar dynamics reach asymptotic length rapidly and then remain at this size for many years (Choat & Robertson 2002; Newman et al. 1996).

Life History Strategy and Management Implications

Life history traits are classified using many different frameworks (Kawasaki 1980; Pianka 1970; Winemiller & Rose 1992) that can be used to predict how species will respond to disturbance or management (King & McFarlane 2003; Winemiller 2005). For fishes, one approach has been to develop a trilateral continuum model to divide species into three strategic categories: opportunistic (small, short-lived, high reproductive effort, high demographic resilience), equilibrium (low fecundity, large egg size, parental care) and periodic (long-lived, highly fecundity, high recruitment variation) (Winemiller 1989; Winemiller & Rose 1992). In addition, fishes may also exhibit distinct salmonic or intermediate strategies (King & McFarlane 2003; McCann & Shuter 1997).

We used the trilateral framework to understand how the suite of life history traits exhibited by *H. comes* assorted in multidimensional space relative to 113 other temperate and tropical fishes, that varied widely in their ecology and life history. *Hippocampus comes* grouped most closely with tropical equilibrium strategists (Fig. 8), with which it shares traits that relate mainly to reproduction. Seahorses have relatively large mature oocytes, small broods, and substantial parental investment (but not other equilibrium traits). *Hippocampus comes* shares many other traits in common with opportunistic species which tend to be small bodied, mature rapidly, spawn regularly and iteratively. Most of these factors lead to rapid population turnover. Another temperate species of seahorse, *H. guttulatus*, assorted in a similar manner, suggesting that seahorses are a genus with life history strategies broadly intermediate between tropical equilibrium and opportunistic strategists. In a previous analysis that included only temperate species, *H. guttulatus* grouped with opportunistic strategists (Curtis & Vincent 2006), indicating that ordination methods are sensitive to input traits (details in Appendix III).

Hippocampus comes and tropical equilibrium strategists share traits that relate mainly to reproductive behaviours that increase their population-level risk. Developed parental care of large oocytes often corresponds to small broods in equilibrium fishes, that slows their intrinsic rate of increase. Furthermore, sexually monogamous seahorses (Jones et al. 1998; Wilson & Martin-Smith 2007) suffer depressed reproductive output, relative to fishes without mate-pairing, when one partner is widowed by fishing. Management recommended for equilibrium strategists includes (a) maintaining productive habitat that supports healthy adults stocks and promotes surplus yield (Winemiller & Rose 1992) and (b) assuring moderate to low harvest rates (King & McFarlane 2003).

Most of the traits shared between *H. comes* and opportunistic life history strategists (small size, rapid growth, frequent iteroparity and short lifespan) govern population turnover and confer low susceptibility to risk (Roberts & Hawkins 1999). Opportunistic species are predicted to be resilient, provided that management assures refugia (e.g. marine reserves, deep unfished areas) from which protected animals can recolonise disturbed areas (Winemiller & Rose 1992). At the same time, the short generation times of opportunistic species mean that populations may fluctuate rapidly in response to environmental factors, increasing vulnerability to consistent and high levels of extraction during times of depressed abundance (Curtis & Vincent 2006; King & McFarlane 2003).

Non-extractive marine reserves are one management approach that would serve both strategists, protecting spawning stock and habitat while also providing refugia for colonization. Results from this research (Morgan & Vincent 2007) and elsewhere (Project Seahorse, unpublished data) indicate that densities of *H. comes* inside and outside reserves are seldom substantially different. Therefore adult spillover from high densities inside reserves is unlikely. The main benefit of no-take zones to seahorses appears to be protection that allows residents to grow large then make proportionally large contributions to larval emmigrants, compared with individuals already in fishing grounds. Reserves in the Danajon Bank are presently the only mechanism protecting adult *H. comes* and are well-accepted by fishing communities. The existing reserve network may need to be expanded, as well as better enforced, to support current fishing pressure in the area (Samoilys et al. 2007).

Our work indicates that priority research would include obtaining long-term abundance time series, documenting the lifespan of wild *H. comes* and generating further age-at-length data. These data will be necessary to implement effective management. Quantitative modelling will be particularly useful for species such as *H. comes* where intermediate life history traits challenge management recommendations based on broad general frameworks such as the trilateral continuum model (for examples, see King & McFarlane 2003). For *H. comes*, data on population trends and longevity could come from standardized, low-intensity, multi-year, in situ studies in habitats across the species' range. Improving our understanding of growth will require further CMR efforts. Information from large juvenile size classes (40-100 mm) will be important, since growth in these size classes is poorly documented from both ex situ research and in situ surveys. These data will be easiest to obtain if coordinated with the annual recruitment pulse and if focused on wild macroalgal beds where juveniles are most abundant (Morgan & Vincent 2007). CMR design will need to account for rapid juvenile mortality and depletion by fishing. Exclusively length-based analyses of *H. comes* should be avoided given individually variable growth and because cohort progression through upper size classes could be confounded by the effects of seasonal fishing effort, size selective fishing, and variable seasonal abundance.

Methods used in this study are relevant to demographic data collection for other fishes captured in reef fisheries. In particular, using simple, inexpensive, subcutaneous tagging methods to generate CMR information from limited temporal and spatial scales, allowed us to generate first estimates of vital rates that govern growth and survival of *H. comes*. This is an approach that can be used to collect demographic information from relatively sparse populations of rare fishes – sometimes those that most need conservation. Similarly, methods such as CMR can be extended past sedentary species such as seahorses, to sparse fish taxa that exhibit greater mobility and dispersal (Labonne & Gaudin 2005). For reef fisheries, CMR methods may also be preferable to strictly length-based methods, since many tropical and subtropical species have size frequency distributions with obscure age modes, and can also be difficult to age by counting banding on otoliths or scales (Ebert & Russell 1993; Smith et al. 1998). When research funds or time are limited, if little is known about demographic rates throughout a species life history, or when aiming to build demographic models, we also suggest that it may be most pragmatic to gather less extensive data over a greater range of life stages/sizes/ages, rather than more detailed information within a single stage.

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Table 1. Length-length conversion equations used for juvenile, female and male *Hippocampus comes.* Length conversions are given to transform partial body measurement to straight standard length and also to convert straight standard length (SLs) to height (Ht) and curved standard length (SLc). Two relationships are given for trunk length for females and males, corresponding to linear relationships from individuals <20.0 cm and curvilinear relationship from all female/male sizes. df = degrees of freedom, SE = standard error.

Sex	**Conversion**	**Equation**	**df**	**R^2**	***p***	**SE_{slope}**	**$SE_{intercept}$**
Pooled	Ht from SLs	Ht=0.8472*SLs+0.01019	1,108	0.989	<0.0001	0.0083	1.0540
	SLc from SLs	SLc=1.0037*SLs+2.7781	1,108	0.991	<0.0001	0.0092	1.1650
Juvenile	SLs from HL	$\text{Log}_{10}\text{SLs}=0.6826+1.0410* \text{Log}_{10}\text{HL}$	1,96	0.801	<0.0001	0.0641	0.0530
	SLs from TrL	SLs=8.2110+3.1885*TrL	1,91	0.854	<0.0001	3.4260	0.1382
	SLs from TaL	SLs=13.3482+1.5954*TaL	1,91	0.947	<0.0001	1.8413	0.0397
Female	SLs from HL	SLs=-284.695+131.713*LnHL	1,1022	0.911	<0.0001	4.2866	1.2909
(all)	SLs from TrL	$\text{Log}_{10}\text{SLs}=2.4978(1-\text{Log}_{10}\text{TrL}\hat{}-4.3536)$	1,1022	0.901	<0.0001	0.0056	0.0324
(<20 cm)	SLs from TrL	$\text{Log}_{10}\text{SLs}=0.7628+0.8751*\text{Log}_{10}\text{TrL}$	1,990	0.894	<0.0001	0.0096	0.0154
	SLs from TaL	$\text{Log}_{10}\text{SLs}=0.3039+0.9815*\text{Log}_{10}\text{TaL}$	1,1022	0.935	<0.0001	0.0155	0.0081
Male	SLs from HL	SLs=-261.5773+125.0290*lnHL	1,994	0.900	<0.0001	4.4168	1.3196
(all)	SLs from TrL	$\text{Log}_{10}\text{SLs}=2.4813(1-\text{Log}_{10}\text{TrL}\hat{}-4.5212)$	1,994	0.883	<0.0001	0.0057	0.0364
(<20 cm)	SLs from TrL	$\text{Log}_{10}\text{SLs}=0.9277+0.7786*\text{Log}_{10}\text{TrL}$	1,938	0.819	<0.0001	0.0120	0.0192
	SLs from TaL	$\text{Log}_{10}\text{SLs}=0.3185+0.9724*\text{Log}_{10}\text{TaL}$	1,994	0.859	<0.0001	0.0241	0.0125

Table 2. Estimates of growth rates from other syngnathids. Values are from FishBase and modified from Takahashi et al., 2003. NG = Not given in source reference. Brood sizes are given ± one SD. Ex situ refers to rates estimated in aquarium facilities.

Species	Loc'n	T (°C)	In situ/ ex situ	Breeding season	Brood size	K (yr^{-1})	Linf (cm)	Ref
H. abdominalis (male)	Sydney, Australia	19-25	In situ	NG	NG	2.1	19.0	K. Martin-Smith & Burgess-Wilson, unpublished
H. abdominalis (female)	Sydney, Australia	19-25	In situ	NG	NG	1.4	21.0	As above
H. comes	Philippines	NG	In situ	NG	200	1.7	12.0	Perante et al. 1998
H. comes	Philippines	28.5	In + Ex situ	All year	388 ± 172	2.9	16.7	This study
H. guttulatus	Portugal	10-28	In situ	May-Oct	435 ± 116	0.57	19.8	Curtis & Vincent 2006
H. erectus	Bay of Texas	26	In situ	NG	NG	0.34	21.4	Matlock 1992
H. erectus	Florida, USA	25	In situ	July-Sept.	250-300	2.5	14.0	Beverton & Holt 1959
H. kuda	China	NG	Ex situ	NG	NG	2.50	19.2	Mi 1992
H. kuda	Viet Nam	NG	Ex situ	NG	NG	1.04	21.9	Mi 1992
H. zosterae	Florida	25	In situ	Feb.-Oct.	3-25	12	20.0	Beverton & Holt 1959
Nerophis ophidon	Germany	8.2	In situ	NG	NG	1.05	30.4	Worthmann 1975
Stigmatopora argus	Sydney, Australia	19-25	In situ	NG	NG	1.79	17.5	Duque-Portugal 1989
Stigmatopora argus	Sydney, Australia	19-25	In situ	NG	NG	0.84	20.0	Duque-Portugal 1989
Stigmatopora argus	Tasmania, Australia	12-20	In situ	NG	NG	1.44	23.0	Jordan et al. 1998
Syngnathoides biaculeatus	Queensland, Australia	25.5	In + Ex situ	Oct-Apr.	153	2.8	26.0	Takahashi et al. 2003
Syngnathus rostellus	Europe	8.2	In situ	July-Oct.	NG	0.75	20.0	Pauly 1978
Syngnathus typhle	Germany	8.2	In situ	April-Oct.	NG	0.56	26.2	Worthmann 1975
Urocampus carinirostris	Victoria, Australia	12-20	In situ	NG	NG	1.72	10.0	Howard & Koehn 1985
Vanacampus phillipi	Victoria, Australia	12-20	In situ	NG	NG	1.33	12.5	Howard & Koehn 1985

Table 3. A comparison of life history parameter estimates for *Hippocampus comes* between this study and previous research on *H. comes*. VB = Von Bertalanffy, NG = not given in cited reference.

		Life history parameters			
Variable	**Symbol**	**Perante et al. 1998**	**Meeuwig 2001**	**Martin-Smith et al. 2004**	**This study**
Asymptotic length	Linf (cm)	20.3	26	from Meeuwig 2001	16.7
VB growth coefficient	K (yr^{-1})	1.7	0.89	from Meeuwig 2001	2.9
Maximum lifespan	t_{abs} (years)	NG	NG	2.7-3.6	2.7
Natural mortality	M (yr^{-1})	2.81	1.5	0.8-1.6	1.79
Fishing mortality	F (yr^{-1})	2.09	1.6	NG	2.57
Total mortality	Z (yr^{-1})	4.9	3.1	NG	4.36
Exploitation ratio	E (F/Z)	0.42	0.52	NG	0.58

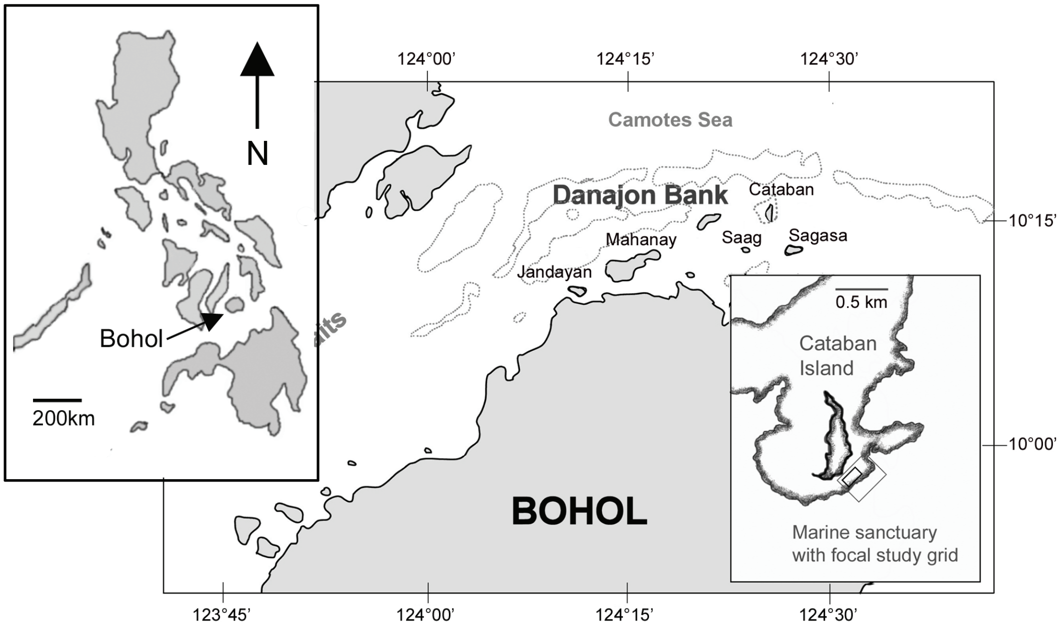

Figure 1. Location of study area, surveyed islands and focal observation grid at Cataban Island, Bohol province, Philippines. Many of the other islands on the Danajon Bank are not shown.

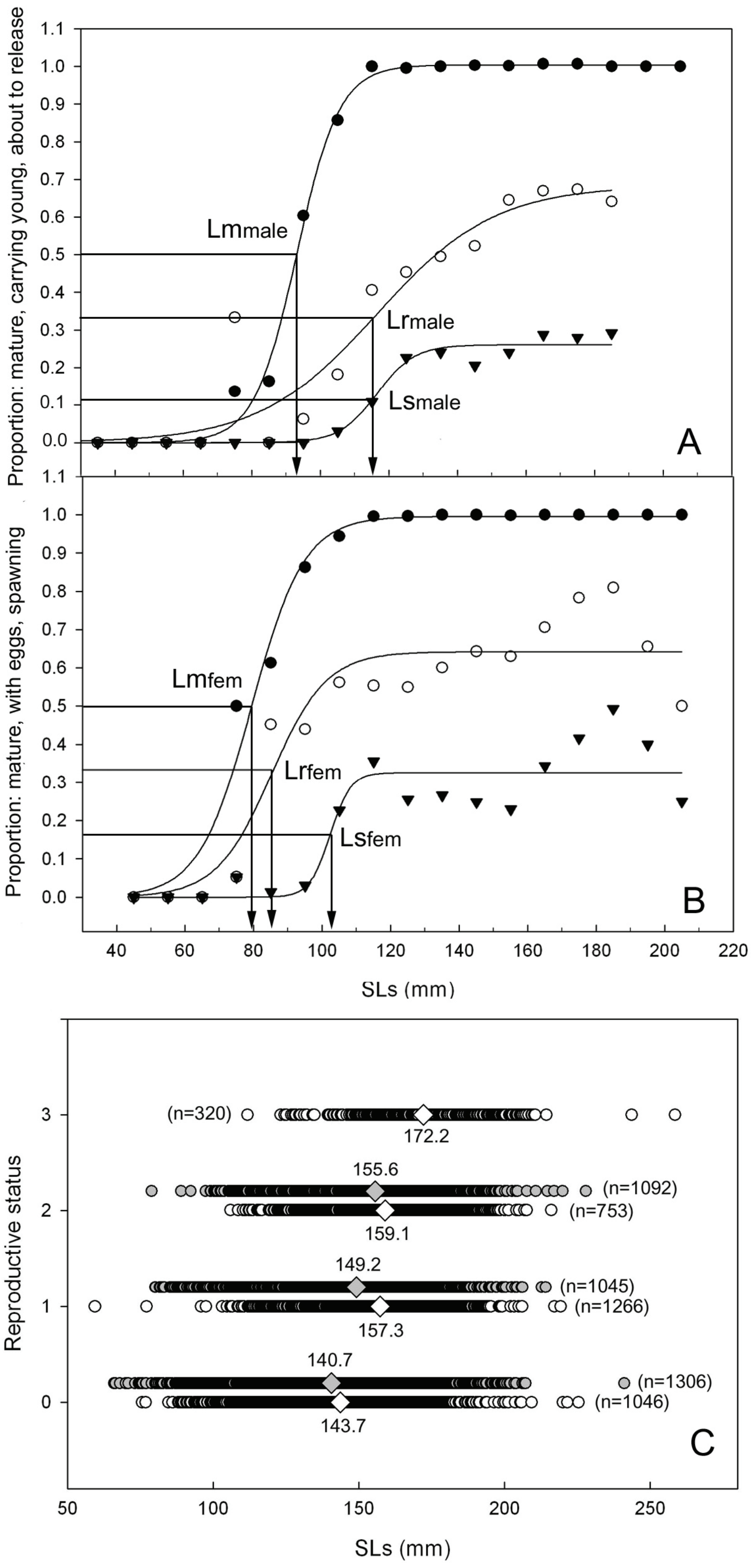
Proportion: mature, carrying young, about to release
Lmmale
Lrmale
Lsmale
A
Proportion: mature, with eggs, spawning
Lmfem
Lrfem
Lsfem
B
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
40
60
80
100
120
140
160
180
200
220
SLs (mm)
Reproductive status
3
2
1
0
(n=320)
172.2
155.6
(n=1092)
(n=753)
159.1
149.2
(n=1045)
(n=1266)
157.3
140.7
(n=1306)
(n=1046)
143.7
C
50
100
150
200
250
SLs (mm)

Figure 2. A) Proportion of males mature (●, RS 0, 1, 2), showing length at 50 % maturity (Lm_{male}). Proportion of males reproductively active (○, RS 1, 2), showing length at 50 % reproductive activity (Lr_{male}). Proportion of males about to release (▼, RS 2), with length at 50 % at release (Ls_{male}) aligned with size at reproductive activity. B) Proportion of females mature (●, RS 0, 1, 2), showing length at 50 % maturity (Lm_{female}), Proportion of females reproductively active (○, RS 1, 2), showing length at 50 % reproductive activity (Lr_{female}). Proportion of females spawning/ passing hydrated eggs to males (Ls_{female}) (▼, RS 2), with length at 50 % transfer not aligned with length at reproductive activity. Abciss in mm SLs. C) Number and distribution of female (●, gray, upper) and male (○, lower) by reproductive status from seahorse landings, Bohol, Philippines (1996-1998 and 2002-2004). Means within female reproductive stage are given by (◆, gray) and within male reproductive stage by (◇). Sample sizes appear beside distributions in brackets.

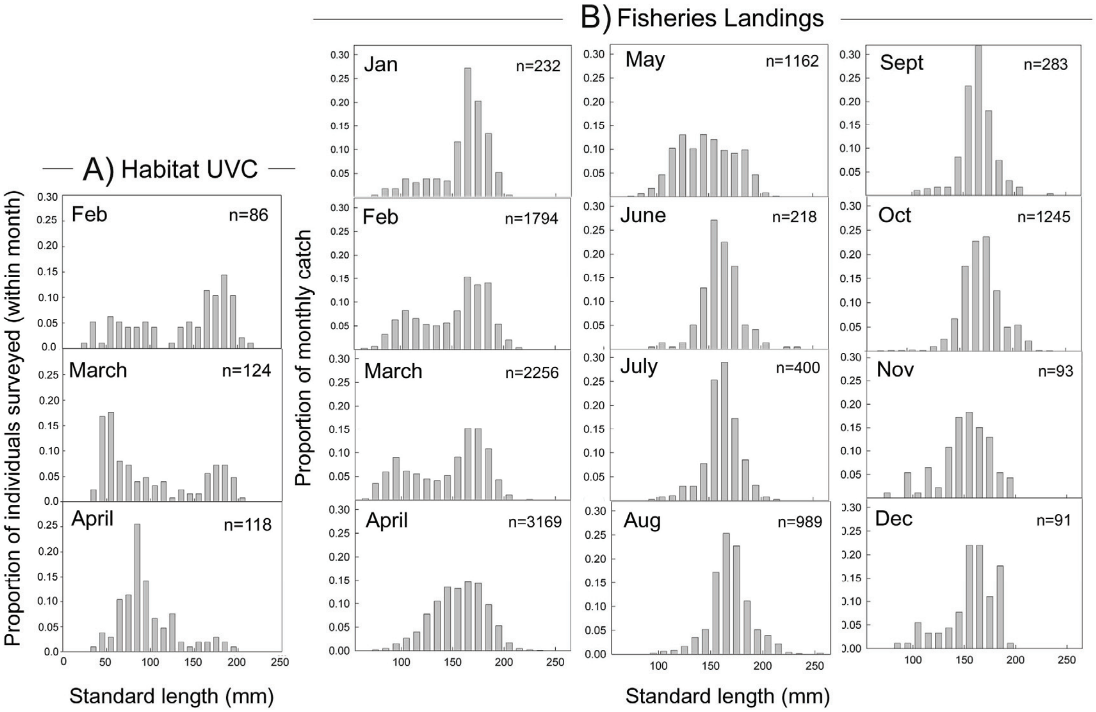

Figure 3. A) Frequency distributions showing the size of individuals present from February–April 2003, from underwater visual census of fishing grounds in coral reef, wild macroalgal beds and farmed macroalgal beds (Morgan & Vincent, 2007). B) Pooled monthly size frequency distributions of seahorses landed at Jandayan Island, Bohol, Philippines, from 1996-1998 and 2002-2004. Sample sizes are given in the upper right corner for each month.

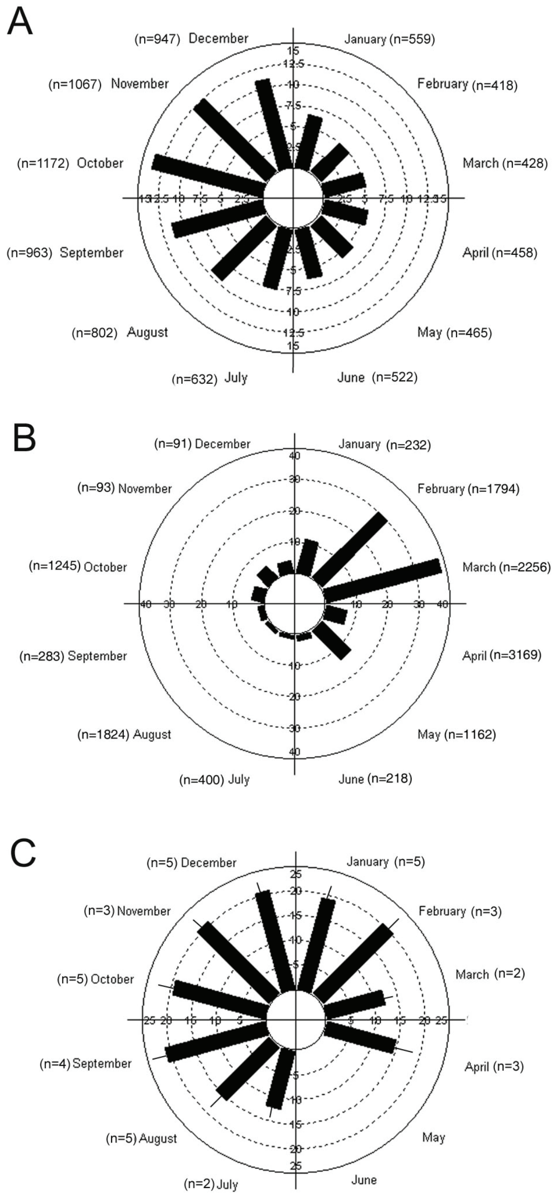

Figure 4. Indices of seasonality in reproduction. A) Percentage of animals inferred via Eq. 6 to have been born by month, based on size and time of catch in landings (1996-1998 and 2002-2004). B) Percentage of total landings that were juvenile by month. C) Duration (days) of mean reproductive cycle by month based on focal grid observations. Months without values represent months without data, monthly sample sizes are given in brackets, and error bars give the within-month SE of reproductive duration (C).

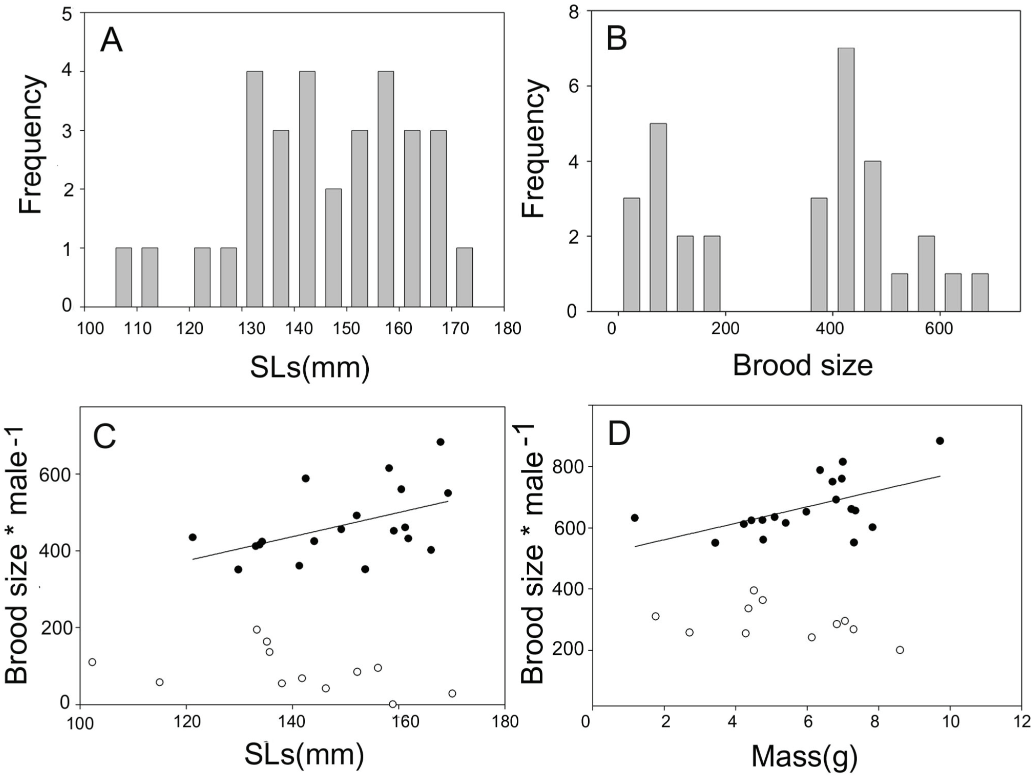

Figure 5. Histograms give A) the relative size distribution of male *Hippocampus comes* (n = 31) used for embryo counts (left) and B) the distribution of embryo counts for all males (right). In scatter plots, C) both straight standard length (SLs) and D) mass showed significantly positive ($\alpha = 0.05$) relationships with embryo number, where ● represent broods from the second mode in histogram B) and ○ represent broods from first mode in B).

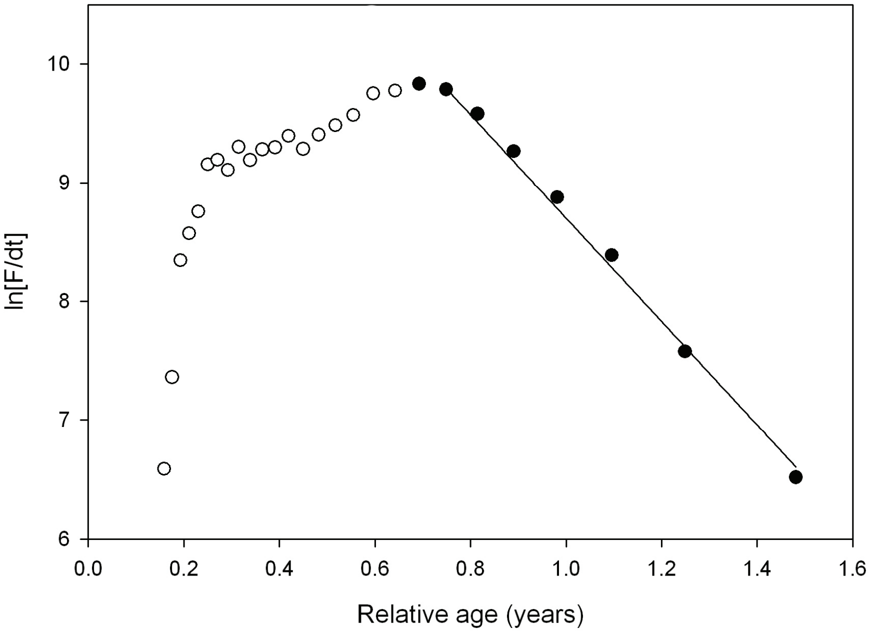

Figure 6. Length converted catch curve from *H. comes* landings, showing instantaneous total mortality, Z, as the slope of the line through fully fished size classes >15.0 cm. Data included in the regression are shown as solid points.

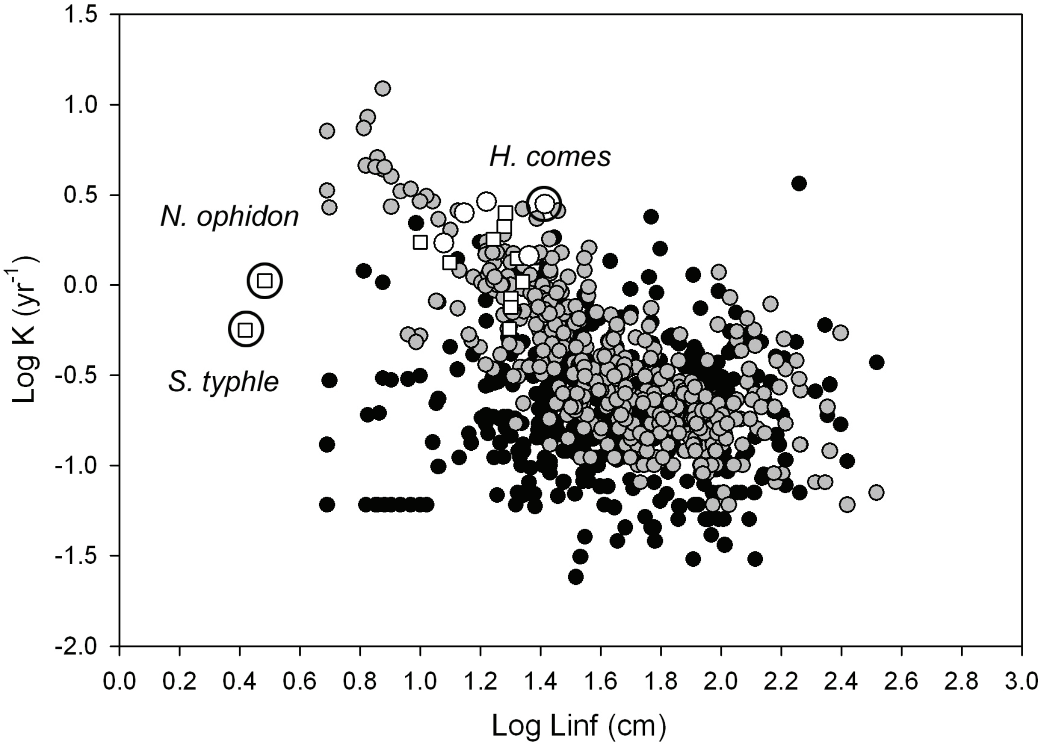

Figure 7. A comparison of syngnathid growth parameters, Linf and K, relative to other teleosts. Syngnathids in warm waters (>25 °C (○) (n = 5)), syngnathids in waters <25 °C (□) (n = 12), teleosts on coral reefs, waters > 25 °C (●) (n = 1574), and 1000 randomly selected teleosts from all environments and all water temperatures to act as a baseline frame of reference (●). Parameters for non-syngnathids were taken from FishBase and values for synganthids were taken from Table 2. Two pipefish species, *Nerophis ophidon* and *Syngnathus typhle*, are circled as outliers (visually identified) with unusually slow growth relative to their length.

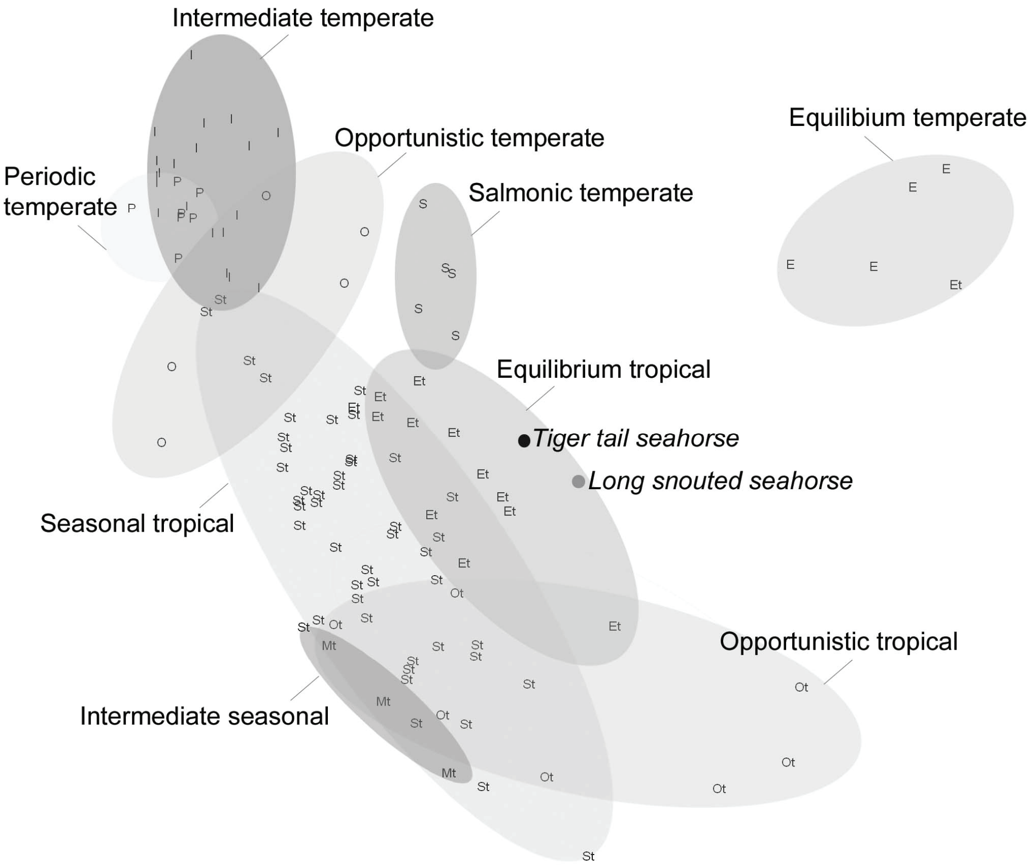

Figure 8. Non-metric multidimensional scaling analysis of 113 temperate and tropical fishes relative to *Hippocampus comes* (●) and *H. guttulatus* (●). Hand drawn ellipses show the position of species with life histories strategies that were assigned by previous research (King & McFarlane 2003; Winemiller 2005; Winemiller 1989). Tropical species are denoted with a t following the main strategy, and temperate species without a t, where: E = Equilibrium, I = Intermediate, M = Intermediate seasonal tropical, O = Opportunistic, P = Periodic temperate, S = Salmonic, St = Seasonal tropical. Descriptions of life history strategies are given in Appendix IV.

Appendix I

Matlab programming code used to estimate the metabolic growth coefficient K, for the Von Bertalanffy growth equation, using maximum likelihood methods described by Wang et al., 1995. Note that text blocks following percentage symbols (%) are comments (not active code), designed to guide the user through functions associated with individual lines of commands.

```
disp('To run this program you must first provide growth data
(mark-recapture pairs), ')
disp('e.g. by running GrowthDataAndPpnJuv2007_xx_xx.m')

global Id Lm Lr T Nfish meanlogLinf stdlogLinf meanlogA stdlogA
% this defines that this basespace and all associated
% function will share a single copy of these variables. Any
% assignment to that variable, in any function, is available to
% all the other functions declaring it GLOBAL.

%In order to get "data" must run GrowthDataAndPpmJuv2007_xx_xx.m

% Codes associated with sources of growth interval data:
1=HandumonX1,
% 2=GridX4, 4/5 = Vietnam ex situ Job et al 2006 and Ky Si
%  Truong, 6=cohort % movement UVC

Id=data(:,1); %the individual seahorse tag numbers
Lm=data(:,2); %vector of starting lengths
Lr=data(:,3); %vector of recapture lengths
T=data(:,4); %is the number of days, measured in fractions of
years, between first and second length measurements

Lr = Lr + 0.001*rand(length(Lr),1);
Nfish = length(T); % the number of cases

results1 = [];
for kk = 2:0.1:4 %for K values ranging from 2 to 4 at increments
of 0.01

    nllkk=    seahorsegrow4(kk);% use the seahorsegrow4 function
for current
    % kk value, now, use the
    meanLinf = exp(meanlogLinf+0.5*(stdlogLinf^2) );
    stdLinf = sqrt( exp(2*meanlogLinf+ (stdlogLinf^2)
    *exp(0.5*(stdlogLinf^2)-1)  );
    meanA = exp(meanlogA+0.5*(stdlogA^2) );
    stdA = sqrt( exp(2*meanlogA+ (stdlogA^2) )
*exp(0.5*(stdlogA^2)-1)  );
    results1 = [results1; [nllkk  kk meanLinf stdLinf meanA stdA
    meanlogLinf stdlogLinf meanlogA stdlogA ]];
```

```
end

% this code can be used for plotting results showing NegLL and
relative NLL as a function of K values

% subplot(2,1,1)
% plot(results1(:,2), results1(:,1),'r:')
% xlabel('k value','fontsize',14)
% ylabel('Neg LL','fontsize',14)
% axis square
% subplot(2,1,2)
% plot(results1(:,2), (results1(:,1)-min(results1(:,1))),'r:')
% xlabel('k value','fontsize',14)
% ylabel('relative Neg LL','fontsize',14)
% axis square

results1

best_k=results1(find(results1(:,1)==min(results1(:,1))),2)
meanlogLinf=results1(find(results1(:,1)==min(results1(:,1))),7)
stdlogLinf=results1(find(results1(:,1)==min(results1(:,1))),8)
```

Appendix II

Matlab programming code used to generate pseudo-confidence intervals around mean asymptotic length ($Linf_m$) estimated via maximum likelihood for the Von Bertanlanffy growth equation.

```
meanloglinf =input(meanlogLinf)
stdloglinf = input(stdlogLinf)
Linfs=(exp(normrnd(meanloglinf,stdloglinf,100000,1)));

sortedLinfs=sort(Linfs);
lower_bound=sortedLinfs(2501)
upper_bound=sortedLinfs(97500
```

Appendix III - Methods Used to Assign the Life History Strategy of *Hippocampus comes*

We compared the life history strategy of *H. comes* relative to other teleosts using vital rates published for tropical (Winemiller 1989) (n = 71) and temperate (King & McFarlane 2003) (n = 43) fish species. We selected five life history traits common to all species for analysis: maximum standard length (fork length, mm), fecundity (brood size), egg size (mean diameter of mature oocytes, mm) generation time (time to fork length at first maturity, years), and type of parental investment. For temperate fishes, generation time was calculated as the time to first maturity using K and Linf values in King and MacFarlane (2003) via the Von Bertalanffy growth equation, while generation times for tropical species were taken from Winemiller (1989). We used observed values of time to first maturity (Lm) for *H. comes* and *H. guttulatus* (Curtis & Vincent 2006). Parental investment was scored from 0 - 14 and assigned based on three factors 1. the protective placement of zygotes/larvae, 2. the time invested by parents in the protection of zygotes/larvae, 3. the nutritive contribution to larvae by parents (Winemiller 1989). Species were ordinated in a two-dimensional space using non-metric multidimensional scaling which does not require data to conform to assumptions of normality. nMDS is designed to preserve the distance between dissimilarities in low dimensional ordination space (Clarke & Warwick 2001).

Appendix IV

Table 1. Life history strategies of temperate and tropical fishes, described by A) Winemiller (1989), B) Winemiller (2003), C) King and MacFarlane (2003), D) McCann and Shuter (1997) and used to contextualize vital rates of *Hippocampus comes* in Figure 8.

Life History strategy	Symbolic notation	Description	Example species	Source
Equilibrium tropical/ **Equilibrium temperate**	Et/E	Larger bodied, large oocytes, low fecundity (small clutches), extended gestation, acyclic spawning, substantial parental investment * offspring^{-1}	Freshwater stingray (*Potamotrygon* sp.)/ Spiny dogfish (*Squalus acanthias*)	A/B
Intermediate temperate	I	Similar population dynamics to opportunistic strategists with rapid and high amplitude changes in biomass, life span greater than intermediate strategists and less than periodic strategists, typically 10-20 years, shorter lifespans than periodic opportunists	Pacific hake (*Merluccius productus*)	C
Intermediate seasonal	Mt	Intermediate between Ot and St	NA	A
Opportunistic, tropical/ **Opportunistic temperate**	Ot/O	Small bodied, low fecundity (small clutches), rapidly maturing, regular iterative spawning, low parental investment * offspring^{-1}, short-lived	Guppy (*Poecilia reticulata*)/ Pacific sardine (*Sardinops sagax*)	A/B,C
Periodic	P	Larger bodied, highly fecund, longer life spans, infrequent recruitment events	Sablefish (*Anoploma fimbria*)	B,C
Salmonic, temperate	S	Larger bodied, low fecundity (small clutches), opportunistic strategists with a freshwater and marine phase	Sockeye salmon (*Oncorhynchus nerka*)	C,D
Seasonal tropical	St	High fecundity (large clutches), slower maturation (long generation time), cyclic annual reproduction, low investment * offspring^{-1}	Stout sardine (*Steindachnerina argentea*)	A

LINKING STATEMENT V

Using data collected in Chapters 2 and 3, Chapter 4 estimated vital rates for *Hippocampus comes* and placed the life history of fast growing, short-lived tropical seahorses in context relative to other temperate and tropical fishes. This first set of comprehensive demographic information for a tropical seahorse may allow us to use *H. comes* to infer aspects of the life history of lesser known congeners. It also allows us to begin considering management options.

The last chapter of this thesis uses the understanding of stage structure within the life history of tropical seahorses, described in Chapters 1-3 and quantified as rates in Chapter 4, to formalize the risk to *H. comes* from heavy fishing pressure in the central Philippines. Using population projection matrices, I explore the effects of potential size limits on population viability and how vital rates associated with different stages of the life history affect consequent population growth. This first formal analysis of population dynamics in a tropical seahorse species should recommend priorities for future demographic data collection and assesses the efficacy of existing and potential management guidelines.

CHAPTER 5

MODELLING TEMPORAL CLOSURES AND SIZE-BASED FISHING OPTIONS TO ADDRESS OVEREXPLOITATION IN AN ARTISANAL SEAHORSE FISHERY

ABSTRACT

Seahorses are one example of the many small fishes associated with tropical reef ecosystems that are exploited for income by artisanal fishers. Trade of seahorses has increased globally from the mid 1980s, with particular pressure exerted on mid-sized and large tropical species. In 2002, seahorses were listed on CITES Appendix II and a genus-wide minimum size limits was proposed as a first practical way for trading countries to avoid overfishing. Here we built a deterministic stage-based model for the tiger tail seahorse, *Hippocampus comes* Cantor, 1850 a species that is heavily fished in the central Philippines. Perturbation analyses under different assumed rates of population growth examined the effects of size-based fishing (10 cm or 14 cm minimum size limits (MSLs) or a 10-14 cm slot size) and temporal fishing closures on extraction of a) adults, b) juveniles, and c) all size classes. Results suggested that when year round fishing occurs at high intensity, slot sizes confer greater population persistence and cumulative catches, than the CITES-recommended minimum size limits, presently favoured by stakeholders. Considered in isolation, MSLs could cause evolutionary size-shifts and are unlikely to provide adequate protection for heavily exploited species. On biological merits, slot sizes should assure the survival of large, fecund seahorses, which elasticity analysis show to be influential on population growth. These or other life stages could also be protected via spatial management. This work is one example of how demographic modeling would help to move regional management of tropical seahorses beyond the interim measure of a generic, genus-wide 10 cm minimum size limit and towards more effective management practices that consider population persistence.

INTRODUCTION

Overexploitation is the principal threat facing populations of wild marine fishes (Dulvy et al. 2003). Fishing has caused, and continues to cause, declines of large pelagics (Baum et al. 2003; Myers & Worm 2003; Pauly et al. 1998; Worm et al. 2006), inshore and benthic fish populations throughout the world (Hawkins & Roberts 2004; Hutchings & Reynolds 2004). Changes are best documented in temperate, industrialized fisheries, but losses have been similarly acute if less well recognized, in tropical systems. On island coral reefs it is estimated that 55 % of fisheries in 49 countries are overexploited and present landings are 64 % higher than can be maintained (Newton et al. 2007). Human population growth, open access to ocean resources and poor governance without well-supported enforcement, mean that fish declines now threaten the protein needs and wellbeing of marginalized communities that rely on reef fisheries, particularly in developing countries. These threats are also growing. By 2050, it is expected that the combined human footprint on island coral reefs will increase 160 % (Newton et al. 2007).

Small scale artisanal fishing fleets, comprising 50 of the world's 51 million fishers, remain poorly understood or managed (Berkes et al. 2001). Guidelines on how to steward the resource base of small scale fisheries are badly needed and should be based on the best available information, recognizing the uncertainties inherent in imperfect data (Sadovy 2005). Often, this will mean proceeding without the luxury of either extensive or long-term datasets to inform management decisions (Castillo & Defeo 2005). However, even in data-poor situations the use of quantitative methods that explicitly acknowledge uncertainty can inform the prioritization of data requirements, and can simultaneously provide a platform from which to build consensus for resource management among diverse stakeholders (Morris & Doak 2002; Westley & Miller 2003).

When sufficient data are available, matrix projection models can be used to provide quantitative analyses of population status, growth rates, extinction risk or the potential efficacy of management options (Morris & Doak 2002). The use of population viability analysis (PVA) has been less common for marine than terrestrial taxa. In oceans, PVA has been used to model low density, long-lived species such as turtles (Crouse et al. 1987; Heppell et al. 1996), sharks and skates (Brewster-Geisz & Miller 2000; Cortes 1999), charismatic species such as pinnipeds (Gerber & Hilborn 2001) or species of commercial importance (Cropper Jr. & DiResta 1999; McDonald et al. 2002; Pertierra et al. 1997), although other work has addressed species such as crabs (Miller & Houde 1998) and seagrass (Bearlin et al. 1999). There is no fundamental difference between PVA methods and those employed by many fisheries models. Relative to temperate taxa, modeling efforts for tropical fishes are scarce. Even a basic understanding of vital rates necessary for predictive modeling, is poor or non-existent for most reef taxa. Exceptions tend to be species of commercial importance such as snappers and groupers (Grandcourt et al. 2005; Newman et al. 1996), but not the many small reef fishes that support tropical coastal communities on a daily basis.

Seahorses and Present Policy

Seahorses are an example of the myriad small, cryptobenthic tropical fishes that face overexploitation and habitat destruction. Seahorse fishing provides small amounts of income to large numbers of small scale fishers in developing countries. There are three main markets for fished seahorses: approximately 90 % are dried and used in traditional medicines or as tonic foods, while the remaining 10 % are traded either alive as aquarium pets, or dried for ornamental curiosities (Vincent 1996). It is estimated that greater than 20 million individuals are traded globally every year (Vincent 1996) and of the 14 species in the main dried trade, all possess either partial or fully tropical distributions (Morgan & Vincent 2006). Tropical seahorses are also threatened by losses of their habitat. Structure used as holdfasts and shelter is regularly destroyed by bottom trawling, blast- and other forms of destructive fishing (Marcus et al. 2007), as well as human activities affecting seabeds such as dredging and sea-filling. Similarly, mariculture of kelp, suspended over reefs may also reduce habitat available to seahorses (Morgan & Vincent 2007). Disturbances that disrupt reefs particularly affect small-bodied fishes such as seahorses that associate with live corals for shelter (Wilson et al. 2006).

Recent expansion of the seahorse trade, coupled with local-scale population declines, prompted CITES (Convention on the International Trade in Endangered Species of Wild Fauna and Flora) signatory nations (Parties) to regulate the international trade in all seahorse species (*Hippocampus* spp.) via an Appendix II listing in November of 2002, which took effect in May of 2004. Seahorses are among the first marine fishes of commercial importance to be supported by an Appendix II listing, which requires that Parties allow only exports that are legally obtained and that do not threaten populations in the wild. In 2004, the Animals Committee offered Parties the option of adopting a 10 cm minimum size limit (MSL) (Notification 2004/033) as one means of declaring that their exports were sustainable (Foster & Vincent 2005), although they could also designate other means. The genus-wide minimum size limit represented a pragmatic tool by which customs authorities could regulate trade without a deep understanding of seahorse taxonomy. Subsequent work, recognizing that seahorses become reproductively active at sizes above physical maturation indicates that a genus-wide minimum size limit of about 14 cm may be more precautionary (Morgan & Vincent 2006). The genus-wide MSL for seahorses was initiated as an interim measure and any MSL will require refinement, as well as evaluation, of its effects on population persistence (Morgan & Vincent 2006). In the Philippines, seahorse fishing was de facto banned in 2005 (under the Republic Act 8550 which interprets that extraction should be arrested for species on CITES listings), despite CITES acceptance of trade that does not jeopardize populations in the wild. Nonetheless, trade surveys suggest that seahorse fishing in the

Philippines continues (Morgan & Vincent 2006). In order to manage the trade openly, analysis of size limits and seasonal fishing as well as other management options should now be undertaken at regional and national scales with relevant species in order to design appropriate regional and national policies.

Objectives

Using best available demographic parameters from an ongoing research program (Meeuwig 2001; Perante et al. 2002; Perante et al. 1998) we evaluated which, among a suite of feasible policy options, might best protect the long-term sustainable use of *Hippocampus comes* Cantor 1850 in the Danajon Bank. This seahorse is heavily fished in the central Philippines and is believed to be broadly representative of tropical seahorses, most of which are of comparable size, associate with benthic structure and are captured in shallow (<100m), warm-waters. Given the uncertainties in data for this population and species, our intention here was not to provide quantitative extraction guidelines, or realistic predictions of extinction risk, but rather, a relative ranking of options. In particular, we used perturbation analyses to compare population dynamics associated with fishing only adults, taken principally in the dried trade, fishing only juveniles taken principally in the aquarium trade, or fishing juveniles and adults together for both trades. For adult harvest, we examined three potential management options: (1) a 10 cm minimum size limit, (2) a 14 cm minimum size limit and (3) a slot size from 10-14 cm. For all of these scenarios, we also explored the effects of variable fishing intensity and temporal closures outside the peak fishing season. Finally, we conducted sensitivity and elasticity analyses to examine which vital rates changes would have the greatest absolute and relative effects on the population growth rate. This approach can help to identify life stages where data collection would be most useful or where management interventions could be most efficient.

METHODS

Study Species

Hippocampus comes Cantor 1850, the tiger tail seahorse, is found at variable densities throughout Asian waters and is categorized as Vulnerable by the World Conservation Union based on declines of 30-50 % in some populations (IUCN 2006). The life cycle of *H. comes* begins when females deposit eggs into the ventral brood pouch of males. After fertilization in the pouch, young develop directly (sensu Balon 1999) and are born 2-3 weeks later as small juveniles. Young disperse planktonically for 5-10 days (Chapter 2), then settle to wild algal beds (*Sargassum* spp.) (Morgan & Vincent 2007). Large *H. comes* can be found in macroalgae or on shallow patch reefs at depths from the low tide line to 3 m with occasional sightings to 20 m (Perante et al. 2002). Adults preferentially associate with holdfasts that include bifurcating corals, branching sponges, submerged tree branches and artificial structure (Morgan & Vincent 2007). Adults are found in socially (and likely sexually) monogamous pairs that have endured beyond 21 months in the wild (Perante, 2002).

Study System and Fishery

All data were collected from the Danajon Bank system, a double barrier reef stretching ca. 145 km across the north and western shores of Bohol province in the central Philippines (Pichon 1977) (Fig. 1). Atolls in the system show predictable zonation with mangroves in the nearshore, followed by seagrass and rubble zones, with wild algal beds and corals in deeper areas.

An active seahorse fishery in the Danajon Bank started in the late 1960s. Fishers reported that catches declined from the mid-1980s onwards (Vincent & Pajaro 1997). Seahorses are collected at night as fishers breath-hold dive by the light of kerosene lanterns anchored to the front of small outrigger canoes (lantern fishing). Seahorses and diverse invertebrates are hand-gathered, and fishers also spear edible fishes and cephalopods. *Hippocampus comes* makes up 93 % of seahorse landings, while three other congeners are found only rarely (*H. keloggii, H. kuda* and *H. spinosissimus)* (Perante et al. 1998). The main lantern fishing season corresponds to the inter-monsoon window from February-May, when the weather warms, and water conditions are generally flat with low turbidity, which increases the visibility of benthic targets to fishers. At other times of the year, lantern fishers continue to catch seahorses, but also switch to other targets and use a diversity of other gears that include gill nets, hand nets, and hook and line (jigging).

Model Structure

We used a stage-based model (Lefkovitch 1965) because censused individuals were classified by size but not age, and because for many teleosts, demographic rates are best predicted by size rather than age (Beissinger & Westphal 1998). Given the data presently available for *H. comes*, we constructed an appropriately simple, deterministic and density-independent model to rank possible management options. A conceptual representation of the life history of *H. comes* (Fig. 2) shows the possible fates of individuals moving among four size-defined stages (Table 1). Individuals face one of three fates at each time step: they may die, they may survive and grow into the next stage, or they may survive, grow little and remain in the same stage.

Stage boundaries were chosen based on both their biological relevance and our ability to estimate vital rates with reasonable sample sizes (Table 1). Stages were distinguished based on straight standard length (SLs), which in seahorses is measured as straight-line distances from the tip of the snout to the mid-point of the cleithral ring to the tip of the outstretched tail (Lourie 2003) (Fig. 3). All individuals prior to reproductive maturity were modeled together (Juv, Stage 1). The smallest adult size class ranged from physical maturity (9.3 cm) to the size when *H. comes* transitions from juvenile sponge and macroalgal holdfasts to a wider diversity of adult holdfasts (Morgan & Vincent 2007). This first adult stage, which predominates in wild macroalgal beds was called “Algal Adults” (AA, Stage 2). The second adult stage, “Coral Adults” (CA, Stage 3), ranged from 13.5-17.0 cm and corresponds to sizes that predominate on reefs. These are simple designations that do not attempt to cover all habitats. The final adult stage comprised individuals >17.0 cm that are also found on reefs, but that show greater site fidelity than smaller adults: these were called “Site Faithful Adults” (SFA, Stage 4).

We used a modified form of a birth-pulse formulation with post-breeding census that incorporated low-level, year round reproduction (see the section on growth below). The main projection matrix was built on twelve monthly sub-matrices comprising both seasonally variable and seasonally constant vital rates. The former were different for each monthly matrix, while the latter were the same for each monthly matrix. Vital rates used to build monthly sub-matrices are described in further detail in the parameter estimation section below.

We refer to the composite annual matrix as the base matrix:

$$A = \begin{bmatrix} P11 & F12 & F13 & F14 \\ P21 & P22 & 0 & 0 \\ 0 & P32 & P33 & 0 \\ 0 & 0 & P43 & P44 \end{bmatrix} \qquad (1)$$

where *P*ij values on the sub-diagonal give the probability of surviving and growing to the next stage, and *P* values on the diagonal represent the probability of surviving and remaining in the same stage. No *P*j-1,j terms were included in the model, so individuals could not “shrink”, or revert to an earlier stage. *F*ij are reproductive terms, or the probability that an individual in a given size class, seen at first census, survived to reproduce before the second census. *P* and *F* values are made up of multiple vital rates, and for clarity, will henceforth be referred to as matrix elements. Time steps proceeded in one month intervals.

Data Collection and Parameter Estimation

Vital rates for this study were generated from one year of observations at high intensity. This represents rare information for *H. comes* (or other tropical seahorse species), which are difficult to monitor because of crypsis and low natural densities, further depressed by fishing.

Fecundity

In the Danajon Bank population of *H. comes*, the sex ratio is even (Chapter 4, Perante et al. 2002). Since seahorses in many populations are known to mate size-assortatively (Curtis 2004; Texeira & Musick 2001), we assume that females and males in a given size-stage will be representative of one another. Therefore, we modeled only one sex and also assumed that *H. comes* broods have a 1:1 sex ratio at birth.

Reproductive matrix elements, *Fij,* for each monthly sub-matrix were obtained by multiplying monthly stage-specific survival values (s_t, see Survival section below) by monthly stage-specific fertilities (f_t), calculated as:

f_t = (sex ratio(0.5) *seasonally constant, stage-dependent brood size (bs) * seasonally constant, stage-dependent proportion pregnant (pp) * time-dependent brood number (bn_t)* seasonally constant probability of surviving planktonic stage (s_{rec})).

Brood size (bs) was the number of young incubated per male per pregnancy from the linear relationship between the number of embryos and the length of pregnant males (regression, bs (number of embryos) = -2.69+3.14*(SLs (mm)), $R^2 = 0.24$, p = 0.03, n = 18,) (Chapter 4, Fig. 7). The proportion of males pregnant (pp) for each stage, was calculated as the ratio of males pregnant: not pregnant, associated with the mean size for a given stage. We used the logistic relationship: proportion pregnant (pp) = 0.6835/(1+e(-((SLs(mm)-116.34)/17.2)), $R^2 = 0.91$, $p<0.001$, n = 16) (Chapter 4, Fig. 2). Monthly brood number (bn_t) was calculated from a large fisheries landings dataset (n = 11,928) (Project Seahorse, unpublished data). *First*, we used size at capture, date at capture and a Von Bertalanffy growth model for *H. comes* to back-calculate the estimated birth dates for all harvested individuals (Chapter 4, Fig. 6). *Second*, the total number of broods produced per year was calculated from the number of days between the release of young (reproductive status 3, sensu Perante et al. 2002), averaged within month, then summed over a full year. Reproductive duration was estimated to vary from ca. 14 days in March-July to ca. 20 days in November-February (Chapter 4, Fig. 6). The proportion of total births by month was then multiplied by the mean number of broods per year to estimate the number of individuals born in each month. Planktonic survivorship from birth to recruitment (s_{rec}) presented a challenge because we had no empirical estimates of this value. Therefore, s_{rec} was estimated initially by setting the population growth rate to stationary ($\lambda = 1$), then solving for s_{rec}. The seasonally constant planktonic survivorship term was included in all monthly fertility matrix elements, so that high early mortality was experienced only once by each individual, immediately after birth.

Growth

Since there is evidence that *H. comes* grows to individually variable lengths (Chapter 4), we used a maximum likelihood approach from mark recapture intervals to estimate: (i) a growth coefficient, K, for the population; and (ii) the variation around the mean asymptotic length, Linf, using methods developed by Wang et al. (1995). We assumed that seahorses, like most fishes, exhibit Von Bertalanffy growth:

$$L_t = L\inf^*(1 - e^{-K(t-to)}) \qquad \text{(Eq. 1)}$$

where Linf is mean asymptotic length (cm), K is the metabolic growth coefficient (years^{-1}) and t_o is a theoretical age at which the total length is 0 cm. Growth intervals were generated from five independent data sets that spanned lengths from birth, to 22.0 cm. In situ growth intervals came from the Danajon Bank and included two capture-mark-recapture studies in protected areas (Project Seahorse, unpublished data, Chapter 4), modal progression of cohorts from underwater visual census of fishing grounds (Chapter 4). Ex situ growth intervals came from length-age time series at two aquaculture facilities rearing *H. comes* (Chapter 2, Appendix I; Chapter 4).

Since *H. comes* exhibits a single annual recruitment pulse (Chapter 4) as well as moderate year round reproduction, we created a computer program that allowed us to birth a virtual population of seahorses by appropriate monthly proportions for one year. We then grew these individuals over their lifetimes, simultaneously allowing appropriate proportions to survive according to their size-specific survivorships (Table 1) (Chapter 4). Sizes were converted to stages according to length boundaries given in Table 1, and for each monthly sub-matrix, we calculated the probability of remaining within or growing out, of each stage. These monthly growth transition probabilities, gx (Appendix I, Table 1), were multiplied by survival probabilities (seasonally constant, but converted to monthly values, s_t) to generate *P*ij matrix elements for all sub-matrices in the base matrix (Fig. 2).

Survival

Survivorship for *H. comes* was estimated from a year long mark-recapture study conducted on a focal observation grid, inside a no-take marine reserve located centrally in the northern Danajon Bank, at Cataban Island, from April of

2001 to May of 2002 (Chapter 4). A presence/absence matrix was generated from 68 capture-mark-recapture periods that each represented one full examination of the focal grid. No tagged seahorses were found outside the marine reserve. Annual apparent survival probabilities (Φ) were estimated via an open Cormack Jolly Seber survival model using Program Mark, with the final model formulation selected using Akaike Information Criterion. We examined the effects of sex (male, female), time and size on apparent survival (for details, see Chapter 4, Results or Appendix II). Apparent survival was not significantly affected by season or sex, but did differ among animals of different sizes: annual values, converted to monthly rates (s_t) to include in sub-matrices, are given by stage in Table 1.

Population Size and Quasi-Extinction Thresholds

To initiate simulations, we used a virtual population of 40 000 *H. comes*, estimated to represent the population on the Danajon Bank. Precise bathymetry in this system is unknown (R. Martinez, pers. comm.), so from maps, we visually estimated that ca. 10 % of the total area of the bank area (272 km^2) (Green et al. 2002) was comprised of shallow reef platform suitable for *H. comes*. Densities from fishing grounds in the central northern portion of the Danajon Bank (1.43×10^{-3} individuals m^{-2}, Chapter 3) were applied to total reef area to estimate overall population numbers. These areas were centrally located in the northern portion of the Danajon Bank and comprised approximately 25 % of its length. Quasi-extinction thresholds followed assumptions outlined by Curtis (2004), whereby limited adult movement of *H. comes* (Perante et al. 2002)*,* comparable to *H. guttulatus*, was assumed to be insufficient for animals to find mates at densities less than two animals per hectare. This set the quasi-extinction threshold for the Danajon Bank at 5440 individuals.

Simplifying Assumptions

We made a series of model assumptions that are simplified representations of natural conditions, but that were necessary without data to parameterize more complex model formulations. In particular, we assumed that mean population growth remained constant, so that populations exhibited: a) no demographic stochasticity, b) no density dependence, c) a closed population and d) no temporal environmental trends. All but the latter of these assumptions are discussed in Appendix III.

Fishing Simulations

We undertook a suite of perturbation analyses, looking at four input controls that act to regulate fishing effort. In particular, we examined a temporal closure where the fishery operated only during the season of highest catches, from February-May, and three size-based controls in the form of two minimum size limits and one slot size. Harvesting dynamics were compared based on three metrics: population size after 10 years; cumulative catch after 10 years; and years to quasi-extinction. Ten years was chosen as a convenient time horizon for policy makers and stakeholders. One set of simulations was run for 1000 years to investigate relative values for years to quasi-extinction.

Our scenarios simulated fisheries that were either open year round or only during a four month peak fishing period: both interpretations represent extreme versions of present patterns. A priori, we assumed that year round fishing scenarios would over-represent present fishing potential, both in terms of months fished and the area of the bank subject to comprehensive searching for seahorses, while peak season scenarios would under-represent these factors.

Harvesting simulations were structured to represent extraction from two main trades for seahorses (or both together): exploitation for adults (>10 cm) directed primarily at the dried medicinal trade, and exploitation of juveniles (<10 cm), primarily sold live for the aquarium trade. A third scenario examined extraction of seahorses of all sizes, for both trades.

In simulations, we used both a 10 cm and a 14 cm minimum size limit, because both of these size limits have been recommended to promote sustainability in the international trade of seahorses (Foster & Vincent 2005; Morgan & Vincent 2006). Models were structured to assume that no adults were harvested below minimum size limits (but did include juveniles in “all size” scenarios), and that different proportions of the population were extracted based on fishing intensity, which we modeled for all scenarios at five increments spanning low to high fishing pressure (10 %, 30 %, 50 %, 70 % and 90 %). Fishing intensity was defined as a percentage of the total individuals in a given stage, harvested at each month. We also modeled a slot size that extracted young adults (10-14 cm), leaving the largest adults in the population (Froese 2004). Biologically, the lower boundary of the slot corresponds to physical maturity in *H. comes* while the upper boundary corresponds to the shift from predominantly algal holdfasts to more diverse holdfasts found on reefs (Morgan & Vincent 2007). From a modeling perspective, harvesting this slot size corresponded to the removal of Stage 2 seahorses (“Algal adults”) from the population, making the assumption that fishers identify 10 and 14 cm ± 1.0 cm.

Long-term time series of population abundance are not available for *H. comes*, so we modeled two hypothetical population growth rates, set initially in the absence of fishing, which we call “stable” and “rapid” growth. *First*, for baseline scenarios we set the unfished population growth rate to stable ($\lambda_{\text{theoretical mean}} = 1$), such that fishing automatically caused populations to decline. *Second*, we used the best and only available information on the population growth rate of *H. comes* in the Danajon Bank which is a four-year in situ time series, collected inside a marine protected area from 2002-2005. Without fishing, the average population growth rate corresponded to $\lambda_{\text{In situ mean}} = 1.242$ (Project Seahorse, unpublished data). We refer to this scenario as “rapid growth” since it corresponds to a nine fold increase in population size over a decade. To assure that selected growth rates were reasonable, we gathered literature values of population growth from fishes ranging widely in their distributions and life history traits (Table 2). In situ and literature means for population growth were close ($\lambda_{\text{In situ mean}}$=1.242, $\lambda_{\text{Litt mean}}$ = 1.198). We assume that the two sets of simulations encompass the range of likely long-term mean population growth rate in the wild. Harvesting scenarios for seahorses were intended to evaluate relative, rather than absolute, differences among management options.

Sensitivity and Elasticity Analysis

For the no-fishing base matrix, we identified how changes in different demographic parameters would influence population growth (λ) via sensitivity and elasticity values. Sensitivity measures the absolute impact on population growth, of an infinitesimal change in the transition matrix element aij (examining the local slope of λ as a function of matrix element (aij). Since matrix elements may be measured on different scales, it is also useful to also examine elasticity values, which measure the proportional change in lambda given a proportional change in a vital rate (Caswell 2001).

We calculated sensitivities and elasticities for all underlying vital rates, rather than for matrix elements, which are composites of biologically distinct vital rate values (Mills et al. 1999). Since we report elasticities for vital rates, rather than matrix elements, our elasticity values do not necessarily sum to one. To assure that qualitative patterns were robust to our uncertainty about s_{rec} over a large (more than plausible) range of variation in realized λ, we halved and doubled planktonic survivorship under stable conditions, to examine how extreme lower ($\lambda = 0.692$) and upper ($\lambda = 1.863$) theoretical values of population growth affected the sensitivities and elasticities of vital rates.

RESULTS

Fishing Simulations

Population Size

Assuming stable population growth (neither increases nor declines) (λ = 1), population size after 10 years was often twice as large, or larger, when seahorses were harvested using a slot size, than when using either of the two proposed minimum size limits (10 cm and 14 cm) (Fig. 4). Using slot sizes, abundances declined in a largely linear manner with increased fishing intensity, while minimum size limits caused negative exponential declines (Fig.s 4A, 4B, 4C, 4D). This pattern held when fishing was constrained to the peak season, but the initial decline was less pronounced. After 10 years, at most fishing intensities and particularly at high exploitation (70-90 %), there were few differences in population size (regardless of temporal closures) using MSLs: in all cases populations had declined to near zero. In contrast, remaining population size at high fishing intensities (for adults and all size classes) was more than twice as large when slot sizes were applied in conjunction with temporal closures (Fig. 4B, 4E) than if the fishery was open all season (Fig. 4A, 4E). Since neither size limits nor slot sizes were applied to a fishery focused on juveniles, abundance after 10 years exhibited close to linear relationships with fishing intensity (Fig. 4C, 4D).

When population growth was rapid (λ = 1.242) (Fig. 5) total size of fished populations after 10 years always increased from the baseline (40 000), and maximum abundances were one order of magnitude larger than under conditions of population stability (λ = 1). Regardless of population growth rates, slot sizes always conserved more animals alive than minimum size limits. The relationship between abundance and fishing intensity was similar (in a relative but not absolute sense), under stable and rapid population growth rates and between open and partially-closed fishing seasons (Fig. 4, Fig. 5A, 5B).

Cumulative Catches

Cumulative harvests varied substantially depending on harvest regimes and the temporal dynamics of fishing. When population growth was stable ($\lambda = 1$), 10 cm MSLs always yielded slightly greater catches (1.1-1.6 times more) than 14 cm MSLs (Fig. 6). After 10 years of harvesting, catches from MSLs tended to plateau with increasing fishing intensity, often not yielding greater cumulative harvests with more fishing, because populations had been fished down to quasi-extinction in <10 years (Fig. 7). In contrast, cumulative catch from slot sizes increased in a positive and generally linear manner with increasing fishing intensity, since populations were harvested at rates allowing ongoing reproduction to contribute new individuals to the population that could be taken as catch over the short term (Fig. 6). Temporal closures affected how different fishing strategies optimized catch under different fishing intensities. When animals (catches including adults) were harvested year round, slot sizes yielded greater catches at fishing intensities above 50 % (adults) and above 70 % (all sizes). However, if the fishery was only open for the peak fishing period, slot sizes outperformed MSLs only at very high (90 %) fishing pressure (Fig. 6B), when they yielded 1.2 times more catch than a 10 cm MSL.

Under certain harvest regimes, temporal closures of stable populations ($\lambda = 1$) actually yielded similar or greater catches than year round fishing. In scenarios simulating adults harvests (adults alone, all sizes, Fig. 6), MSLs yielded comparable or greater numbers of individuals at high fishing intensities, if populations were fished only from February-May, rather than in all months (Fig. 6A vs. 6B and 6E vs. 6F). In contrast, when slot sizes were applied, year round fishing always yielded greater catches than harvests with a temporal closure (1.3-2.3 times more depending on fishing intensity). Similarly 1.8-3.3 times more juveniles were caught when fishing occurred in all months versus opening the fishery only in February-May (Fig. 6C, 6D).

When populations were growing rapidly (λ = 1.242), catch dynamics differed from those under population stability (λ = 1). Instead of asymptotic or positive linear dynamics, catches exhibited at least short-term hyperbolic relationships with fishing pressure, and were generally optimized at intermediate levels of fishing (Fig. 5). Hyperbolic yields were observed for slot sizes when fishing was open year round (Fig. 5C), and for minimum size limits when fishing occurred only during the peak period (Fig. 5D).

Under rapid growth (λ = 1.242), fishing intensity and the seasonal duration of fishing influenced whether minimum size limits or slot sizes optimized catches. When animals were harvested year round, minimum size limits generated greater catches up to approximately 35 % fishing intensity, whereas slot sizes were best used for more intense extraction. In contrast, if the fishery operated only during the peak period, MSLs produced greatest yields up to 70 % fishing pressure and slot sizes would generate more catch only under intense (90 %) fishing (Fig. 5C, 5D).

Years to Quasi-extinction

In all scenarios where baseline λ was set to 1, any fishing predictably resulted in declines; these reached quasi-extinction thresholds over periods that varied from a high of 463 years (fishing for juveniles during the peak season only) to a low of 2 years (fishing for juveniles + adults >14 cm all year round) (Fig. 7). Quasi-extinction thresholds were reached most quickly when fishing was intense and fisheries were active all year. In scenarios with adult harvest (adults, all sizes), populations reached quasi-extinction thresholds approximately 4.5 times more quickly (mean ± SD = 4.46 ± 0.72) (Fig. 7A, 7B, 7E, 7F) when animals were harvested via MSLs versus slot sizes. There was little difference in years to quasi-extinction between 10 cm versus 14 cm MSLs, particularly at fishing intensities >30 %. The actual difference in time to quasi-extinction between 10 and 14 cm MSLs varied only between 0 and 5 years. Were only adults caught, populations would decline on average (over all fishing intensities) 6.67 ± 0.92 times more quickly than when only juveniles are fished (Fig. 7A, 7B vs. 7C, 7D).

When compared on the basis of potential population declines, slot sizes were markedly more precautionary than MSLs for populations experiencing positive growth (Fig. 5, $\lambda = 1.242$): only one slot size scenario resulted in quasi-extinction over 1000 year simulations (Fig. 5E, year round fishing, 90 % intensity). In contrast, in most scenarios, MSLs drove populations to their quasi-extinction thresholds within anywhere from 2 to 369 years depending on population growth rates, fishing intensity and temporal closures. The corollary to these patterns is that at rapid (Fig. 5, $\lambda = 1.242$) rates of population growth, many of the simulated fishing scenarios resulted in populations that maintained positive growth with exploitation: particularly when slot sizes were used (Fig. 5: $\lambda>1$ in 53 % of open season simulations and 67 % of peak period simulations).

Sensitivity and Elasticity Analyses

Sensitivity values ranged over six orders of magnitude, with planktonic survivorship exhibiting the largest sensitivity of all vital rates (Fig. 8). Reproductive sensitivities tended to be low, while survival and growth transitions exhibited intermediate values. Differences among the sensitivity of vital rates were amplified when population growth was negative ($\lambda = 0.692$) and reduced when populations were growing extremely quickly ($\lambda = 1.863$). The elasticity values of survival rates were large compared with values for growth and fertility inputs, and the survival of large site faithful adults (S4) was particularly influential. When populations were in decline ($\lambda = 0.692$), the importance of the survival of site faithful adults increased, relative to other life stages. When populations were growing more quickly, the survival of juvenile stages (S1, S2, S3) exerted relatively (but not absolutely) more influence than the survival of large site faithful adults. Annual brood numbers (BN) and planktonic survival

(Srec) also exhibited moderate elasticities at most population growth rates (Fig. 8).

DISCUSSION

Here we undertook a first quantitative evaluation of alternative feasible management measures to manage extraction by artisanal seahorse fisheries. The analysis used a simple deterministic stage-based model that divided the population by age and size to realistically represent the life cycle of the tiger tail seahorse, *H. comes*. Results suggest that when year round fishing occurs at high intensity, slot sizes confer greater population persistence than minimum size limits (MSLs). Slot sizes promote the survival of large, fecund adults, which are influential on population growth. The efficacy of individual policy options will be contingent on stakeholder objectives (e.g., population protection, optimizing catch or avoiding quasi-extinction thresholds), and will also depend on population growth rates, fishing pressure, and catch regimes. This research represents iterative progress in ongoing efforts to improve management of the largely data-poor, but heavily exploited fish genus *Hippocampus*.

Harvesting Implications

Evaluation of a suite of potential policy options for *H. comes* in the Danajon Bank suggests that when heavily fished populations are in states that range from stability ($\lambda = 1$) to rapid population growth ($\lambda = 1.242$), slot sizes are a more precautionary approach to management than MSLs, from the perspective of population persistence. With year round fishing, slot sizes also result in greater cumulative catches at high fishing intensities over even short time horizons such as 10 years, so could also represent a favoured option by fishers. At low fishing intensity (10 %), and rapid population growth ($\lambda = 1.242$), MSLs may generate the greatest catches without jeopardizing stock sustainability. However, fishing mortality in at least the northern section of the Danajon Bank, where seahorse fishing has been most active, is high, with exploitation ratios (total mortality/fishing mortality) of 0.58 (Chapter 4). Without a firm understanding of either population growth rates or fishing intensity, the use of slot sizes for harvesting seahorses in the Danajon Bank would represent a precautionary approach to management.

Compliance

The effectiveness of management measures depends both on ease of implementation and compliance (Bohnsack 2000). During past consultations with stakeholders, slot sizes have been ranked poorly by stakeholders (Martin-Smith et al. 2004), based on the perception that profits would be lost without the catch of the largest, and most valuable size classes that can be captured using MSLs (Foster & Vincent 2005; Vincent 1996). However, management options were compared in the absence of information about catch persistence or cumulative catch. Findings here indicate that the security of fisheries as well as the overall number of fish landed (in most probable scenarios) are likely to be increased, not decreased, using slot sizes versus MSLs. Income from a larger and sustainable take of smaller animals versus diminishing returns from overfishing larger animals could alter the perceived attractiveness of management options, although fishers often discount the worth of future earnings in favour of present income (Goulder & Stavins 2002). Also, because larger fishes tend to be worth disproportionately more than small ones, economic analysis of cumulative profits will be needed for effective ongoing stakeholder consultation.

In the Danajon Bank, 90 % of consulted fishers (n = 101) supported the concept of temporal closures (without any discussion of closure periods) (Martin-Smith et al. 2004). Therefore, it may not be difficult to obtain the voluntary compliance of fishers to take seahorses only during the peak fishing period. Traditional medicine traders in Hong Kong were similarly supportive (Martin-Smith et al. 2004), perhaps because dried seahorses are easily stockpiled and from diverse international sources with varied fishing seasons. All other stakeholders, which included the members of various technical groups on seahorses and the aquarium trade, ranked temporal closures as moderately favourable options on a low - moderate - high scale (Martin-Smith et al. 2004).

Ecological Implications

While MSLs do not augment present fishing pressure on large individuals or large species (because both are currently fully exploited when encountered) (Foster & Vincent 2005), slot sizes have the potential to reduce pressure on the largest and most fecund individuals. In seahorses and other fishes (Froese 2004), individual fecundity is positively correlated with adult size (Texeira & Musick 2001; Woods 2005). Large parents of *Hippocampus kuda*, a sympatric congener of *H. comes*, are known to produce offspring with postnatal growth that is significantly higher than the offspring from younger and smaller parents (Dzyuba et al. 2006). Under ex situ conditions, the young from larger parents also exhibited increased rates of survivorship, relative to the young from smaller parents (Dzyuba et al. 2006). We have also observed that large *H. comes* males produce both a greater number of young (Chapter 4) and larger offspring than smaller fathers (S.K.M, unpublished data).

By allowing removal of the oldest, largest, and fastest growing individuals in populations, MSLs may promote evolutionary shifts favouring the survival of younger, smaller or slower growing individuals (Swain et al. 2007). Research from commercial fisheries shows that populations subject to the removal of large fishes exhibit declines in fecundity, egg volume, larval size at hatch, larval viability, larval growth rates, food consumption, food conversion efficiency, vertebral number and willingness to forage (Walsh et al. 2006). The positive relationship between adult size and juvenile condition suggests that in seahorses, the precursors for similar types of maladaptive selection exist, and should be considered when evaluating potential policy options.

Management Implications

Analyses presented here represent next steps that could be usefully undertaken by scientific authorities in exporting countries to improve national management of seahorse populations. Model outputs should not be perceived as incompatible with recommended international size limits. Rather, the CITES-recommended genus-wide 10 cm MSL presently functions as a pragmatic, but incomplete, first step to data-depauperate management for countries without a history of monitoring seahorse populations. Even as the recommendation was being developed, it was recognized that "the conservation impacts of (10 cm MSL) size restrictions will be better evaluated with a greater understanding of seahorse life history, population dynamics and selectivity of fishing with respect to size and sex" (Foster & Vincent 2005). When countries undertake regional analyses of specific fisheries, these then represent best available information and changes should be implemented, contingent on the approval of stakeholders. Countries have this flexibility since they may provide non-detriment findings (scientific evidence that extraction is not detrimental to populations in the wild), by means of their choosing, to uphold CITES obligations.

Elasticity analysis indicated that survival values exert the strongest relative effects on population growth. Therefore, diminishing mortality - particularly of large site faithful adults - will be the most efficient way to increase the abundance of *H. comes* in the Danajon Bank. This could be accomplished via slot sizes to protect large "mega-spawners" (sensu Froese 2004), alone or in combination with spatial management. Most existing marine protected areas in the region protect coral reefs, used by adult *H. comes* (Morgan & Vincent 2007; Perante et al. 2002): animals inside reserves reach larger sizes than animals in fishing grounds (Project Seahorse, unpublished data). However, it remains unclear whether the cumulative protection provided by the network of small reserves in the Danajon Bank is sufficient to assure population persistence in the face of extensive fishing. Where communities could be reluctant to further reduce fishing in reef areas (which are vital for many fisheries), they are proving receptive to inclusion of other habitats (A. Vincent pers. comm.) such as the reef-fringing wild macroalgal beds that are inhabited by smaller size classes (Morgan & Vincent 2007).

Scenario outputs point to the importance of measuring a) fishing intensity, and b) system-specific population growth rates, which both exert strong influence over population dynamics. Anecdotal information indicates that strong fishing pressure on the Danajon Bank has caused local declines of *H. comes* populations from 65 to 100 % over periods of 20 years or less (A. Maypa unpublished data, in Morgan & Vincent, 2006). Data on fishing intensity (fishing effort time^{-1} area^{-1}) is necessary for stakeholders to compare policy options.

Long-term monitoring of population abundance (e.g. 10+ years) will be necessary to quantify trends in population growth rates reliably (Morris & Doak 2002). Abundance time series presently available for seahorses are short and even 3-5 years of information is rare. These data will be particularly important if seahorses experience cyclic, multi-year fluctuations in abundance. Evidence from at least five seahorse populations indicates that abundance can vary by one or more orders of magnitude over periods from 4-7 years, under constant or no fishing pressure (S. Morgan, pers. obs.,de Silva et al. 2003 in Curtis 2004; Larkin & Adams 2003; Martin-Smith & Vincent 2005). Vital rates or population trends estimated from subsections of population cycles could therefore misinterpret both risk and resilience. Abundance trends from unfished areas would be the best way of providing this information, but fisheries dependent metrics such as catch per unit effort (e.g. seahorse catch per fishing hour) could also act as useful proxies. This information need not require complex sampling or intense effort - one standardized annual census of sufficient power, at a set time of year, is adequate to quantify inter-annual trends.

If other tropical seahorses have comparable demography to mid-sized *H. comes*, results suggest that the 10cm MSL for seahorses in international trade - currently recommended as an interim and generic management measure by the CITES Animal Committee - will not per se provide adequate protection for either large-bodied or heavily harvested species. This issue will be particularly problematic for tropical seahorse species, which make up the majority of seahorses in international trade. Managers charged with fisheries responsibilities would benefit from more (and in some cases any) basic demographic data (survival, growth and reproduction), spatial and temporal quantification of fishing effort and multi-year abundance time series.

At least two main constraints should be considered when using PVA (or most other single-species modeling approaches) in poorly understood and multi-species marine fisheries. First, PVA requires substantive demographic information, often not available for species in reef fisheries (discussed in Chapter 4). Nonetheless, as shown here, PVA can use data inputs of variable quality and outputs can be evaluated from a relative versus absolute perspective. Second, PVA is inherently a single-species modeling approach, but can in theory, be extended to multiple species by combining habitat suitability maps with spatially-explicit threat weightings (Akcakaya 2000). However, most coral reef communities are highly speciose, with few individuals per species, such that assemblage- and community-based approaches may be most valuable. This is particularly true when capture is inherently non-selective, as it is in the many reef fisheries (not for seahorses) that rely on blast-fishing or trawls (Edinger et al. 1998; McManus 1997; White et al. 2000). Similar considerations are also prompting ecosystem-based approaches for temperate demersal and pelagic fisheries (Marasco et al. 2007).

PVA remains useful for assessing reef fisheries, even when demographic inputs are limited, to prioritize among management options and to model targeted species such as those captured by hand or with selective gear. In data-limited situations, assessing the viability of flagship species such as seahorses can be used to incite management action and to provide umbrella protection (e.g. spatial closures) for other sympatric organisms, unlikely to be managed based on their own demography

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Table 1. Stage classes used in main projection matrix, depicted in Fig. 2, and associated size-based vital rates. Stages were defined based on shifts in; physiology (e.g. juvenile versus adults), habitat use (algal adult versus coral adults) and behaviour (site fidelity). Size is given as straight standard length. Stage-based survivorships were seasonally constant so are given as annual rates, but were converted to monthly values (s_t) for inclusion in sub-matrices. Note that fertilities were multiplied by 0.5 because we modeled only one sex and the sex ratio in the population was even.

Stage	**Stage name**	**Size (SLs cm)**	**Age**	**Stage-based survivorship (yr^{-1})**	**Confidence intervals, survivorship**	**Stage-based fertility (# young brood^{-1})**	**Proportion breeding by size**
	Juv, Planktonic	1.0-3.0	birth-10 days	Srec = 0.0014 ($\lambda = 1$) Srec = 0.0019 ($\lambda = 1.242$)			
1	Juv, Settled juveniles	1.0-9.3	birth-4 mo.	0.03151748 (50-96 mm)	1.11319 X 10^{-3}-0.35346	253.1	0.0795
2	AA, Algal adults small adults	9.3-13.5	~4-8 mo.	0.104317962	0.02518-0.24991	378.1	0.3905
3	CA, Coral adults mid-sized adults	13.5-17.0	~8 mo.-variable	0.104317962	0.02518-0.24991	491.9	0.6263
4	SFA, Site Faithful Adults, large adults	>170	variable	0.452956331	0.18506-0.68967	572.6	0.6698

Table 2. Uppermost and lowermost population growth rates from projection matrix models of fishes and elasmobranches, available in the published literature. “Low” and “high” values denote 95% confidence intervals around the overall mean among species.

Species, common name	**Species, Latin name**	**Bathymetric distribution and range**	**Population growth rate, (λ)**	**Reference**
Whale shark	*Rhincodon typus*	Pelagic, global	0.7177-1.2658	Bradshaw et al. 2007
Wooly sculpin	*Clinocottus analis*	Intertidal, temperate	0.3-3.6	Davis & Levin 2002
Leopard grouper	*Mycteroperca rosacea*	Inshore, sub-tropical	0.730-1.283	Wielgus et al. 2007
Boccacio rockfish	*Sebastes paucispinus*	Inshore, temperate	0.83-1.13	Tolimieri & Levin 2005
Tilapia	*Oreochromis mossambicus*	Freshwater, tropical	0.9935-1.0027	Liao et al. 2006
Andean catfish	*Astroblepus ubidiai*	Freshwater, temperate	1.0674-1.4614	Velez-Espino 2005
Overall averages			(low) 0.7731 (mean)1.198 (high) 1.6238	

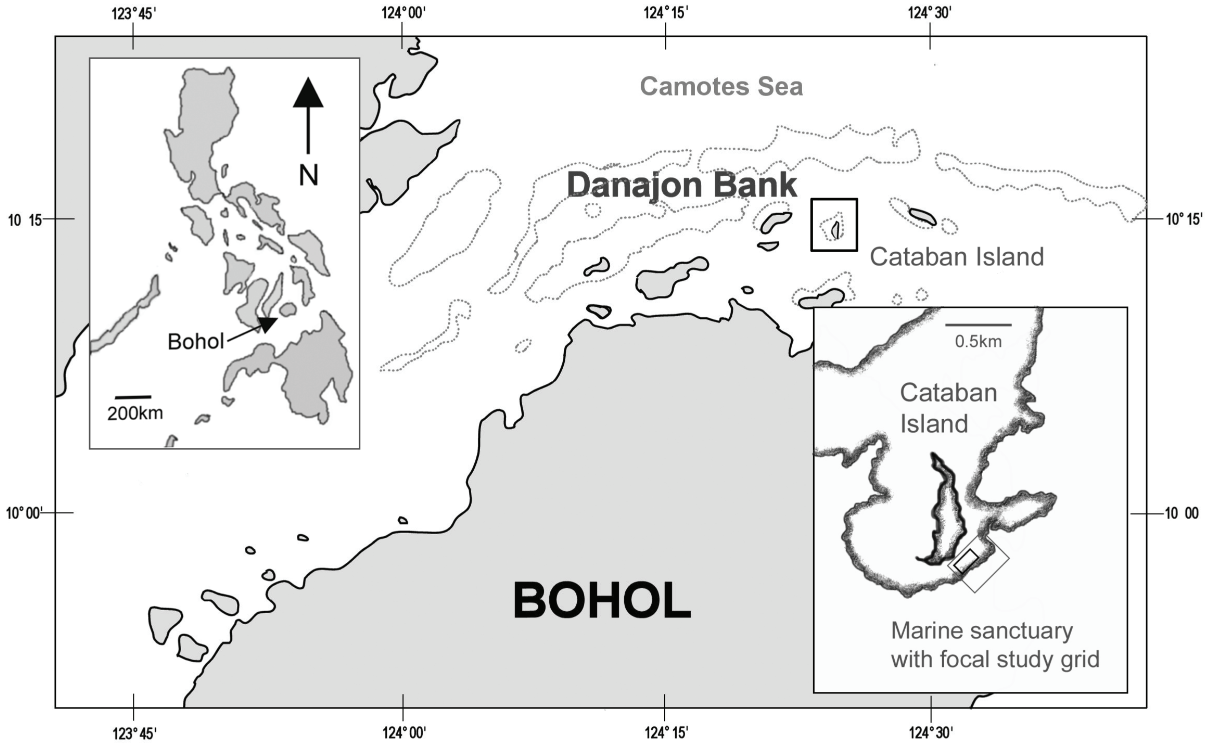

Figure 1. Location of the study site at Cataban Island, Bohol, Philippines (10°13.75'N 124° 23.36'E). The focal observation grid is indicated by the inner rectangle within the no-take marine sanctuary on the southeast edge of Cataban's fringing reef platform.

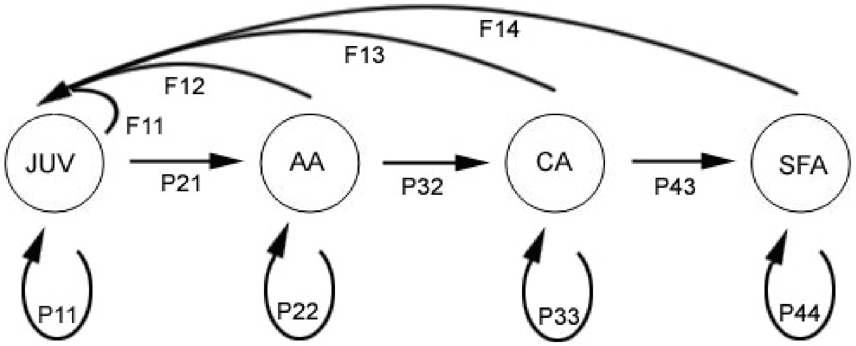

Figure 2. Life cycle diagram of stages used to analyze the prospective demography of the tiger tail seahorse, *Hippocampus comes*. Stages of the life history are represented by circles, where stage 1 = juveniles, stage 2 = algal-dwelling adults, stage 3 = coral-dwelling adults and stage 4 = site faithful adults. Sizes and ages corresponding to stages are given in Table 1. Arrows moving left to right between stages (*P*ij) denote the probability of transitioning between stages, while arrows starting and ending at the same stage (*P*ij) give the probability of remaining in the same stage over a single time step. Fertilities (*F*ij) are given as arrows moving right to left from reproductive stages to the juvenile stage.

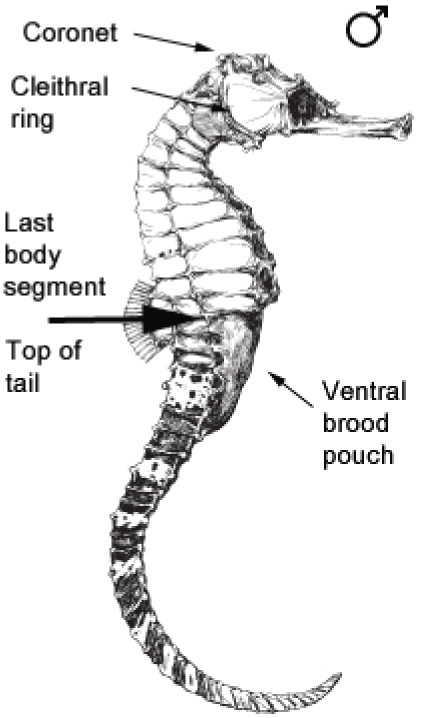

Figure 3. Male *Hippocampus comes*, showing relevant body parts used to define maturity and to measure animals for minimum size limits and slot sizes. Reproduced with permission from Lourie et al. 2004. Illustration by Laurence Richardson.

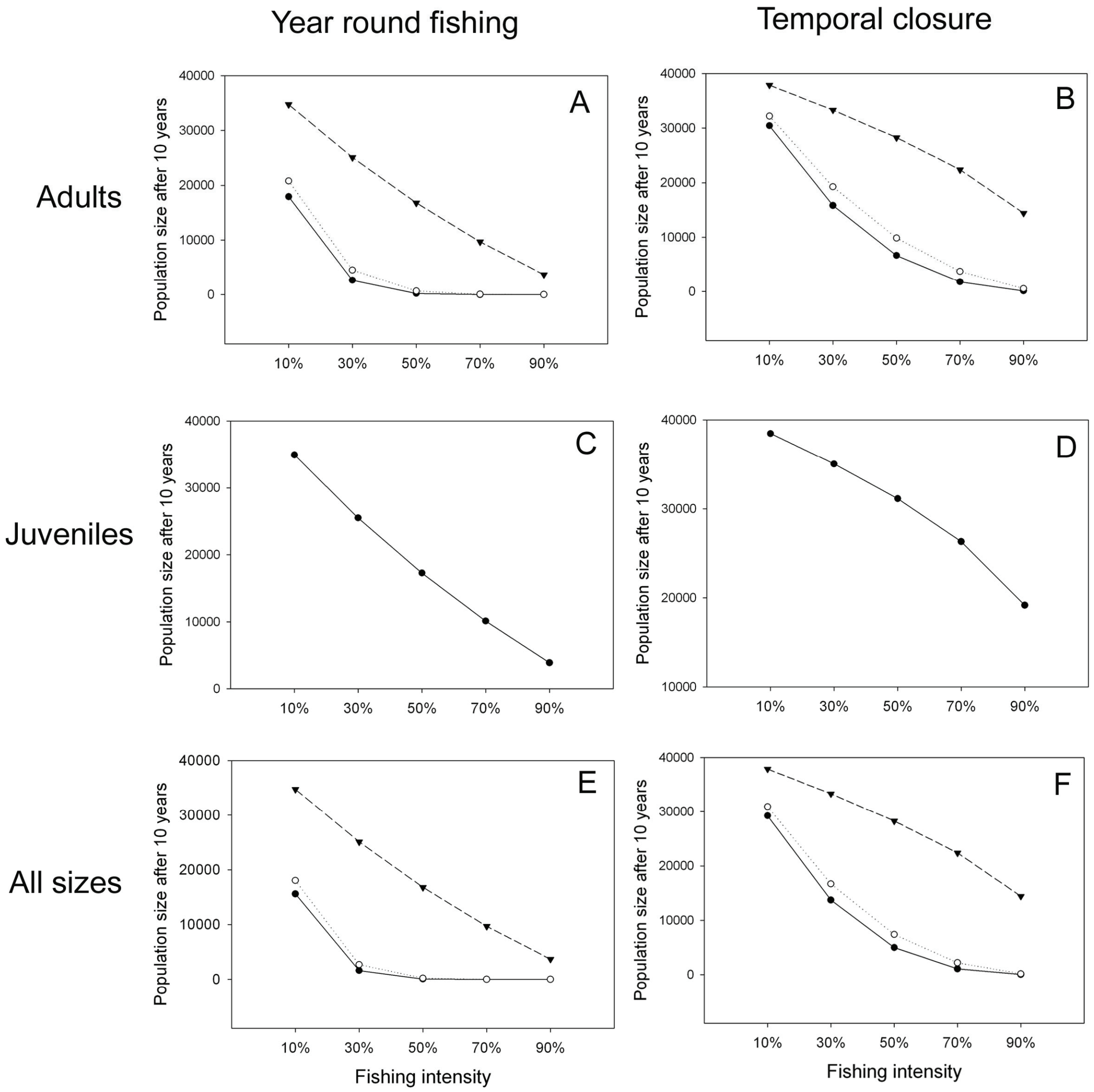

Figure 4. Simulations corresponding to population size after 10 years of harvesting seahorses (*Hippocampus comes*) under three management scenarios, with populations growth set at $\lambda = 1$. Adults (A, B) or all animals (E, F) were collected under a 10 cm minimum size limit (●), a 14 cm minimum size limit (○) and a 10-14 cm slot size (▼), while all sizes of juveniles were captured equally whether alone (C, D) or with adults (E, F). Population size is modeled at five different monthly fishing intensities, exerted on populations throughout the year (left side, A, C, E) or only during the peak fishing season (right side, B, D, F).

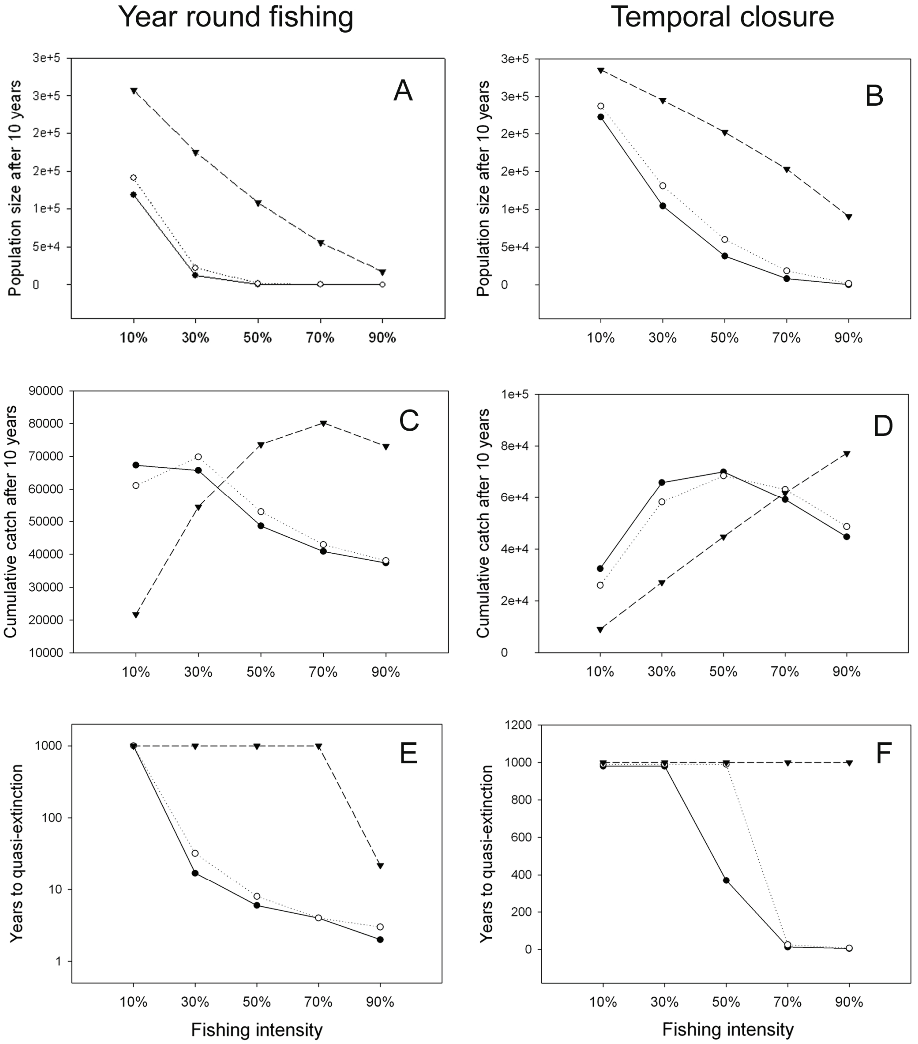

Figure 5. Population size (A, B), cumulative harvest (C, D) and time to quasi-extinction (E, F) of juvenile and adult seahorses (*Hippocampus comes*) after 10 years of fishing at rapid population growth ($\lambda = 1.242$). All juvenile size classes were fished at the relevant intensities, while adults were collected size-selectively via a 10 cm minimum size limit (●), a 14 cm minimum size limit (○) and a 10-14 cm slot size (▼). Fishing was modeled at five different monthly fishing intensities, exerted on populations throughout the year (left side) or only during the peak fishing season (right side). For years to quasi-extinction, values equivalent to 1000 years means that populations did not reach the quasi-extinction threshold during a 1000 year simulation. Note that the ordinate axis in Figure E is on a log scale.

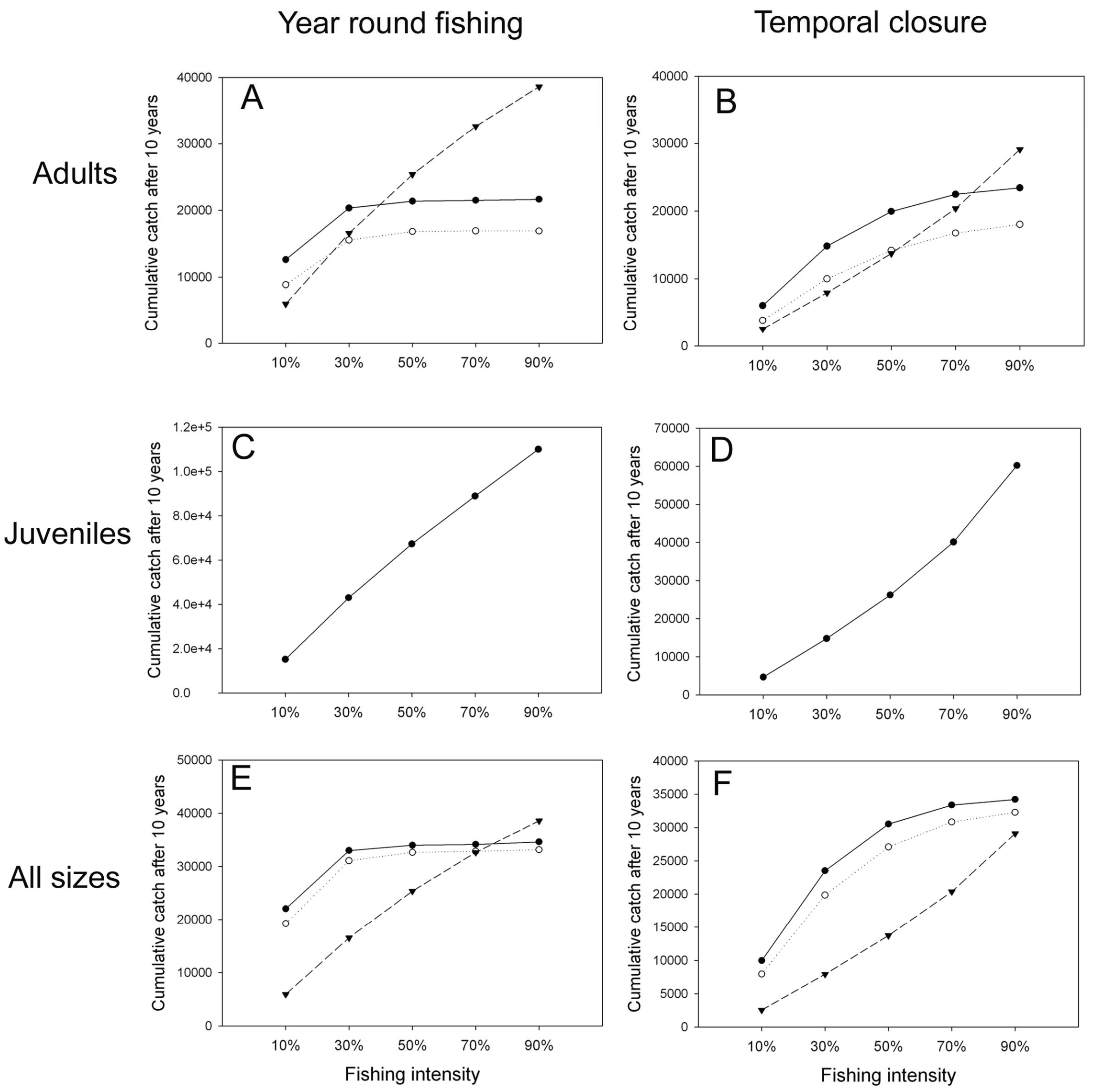

Figure 6. Simulations corresponding to cumulative catch after 10 years of harvesting seahorses (*Hippocampus comes*) under three trade scenarios, with baseline population growth set at λ = 1. Adults (A, B) or all size classes (E, F) were collected under a 10 cm minimum size limit (●), a 14 cm minimum size limit (○) and a 10-14 cm slot size (▼), while all sizes of juveniles were captured equally whether alone (C, D) or with adults (E, F). Population size is modeled at five different monthly fishing intensities, exerted on populations throughout the year (left side, A, C, E) or only during the peak fishing season (right side, B, D, F).

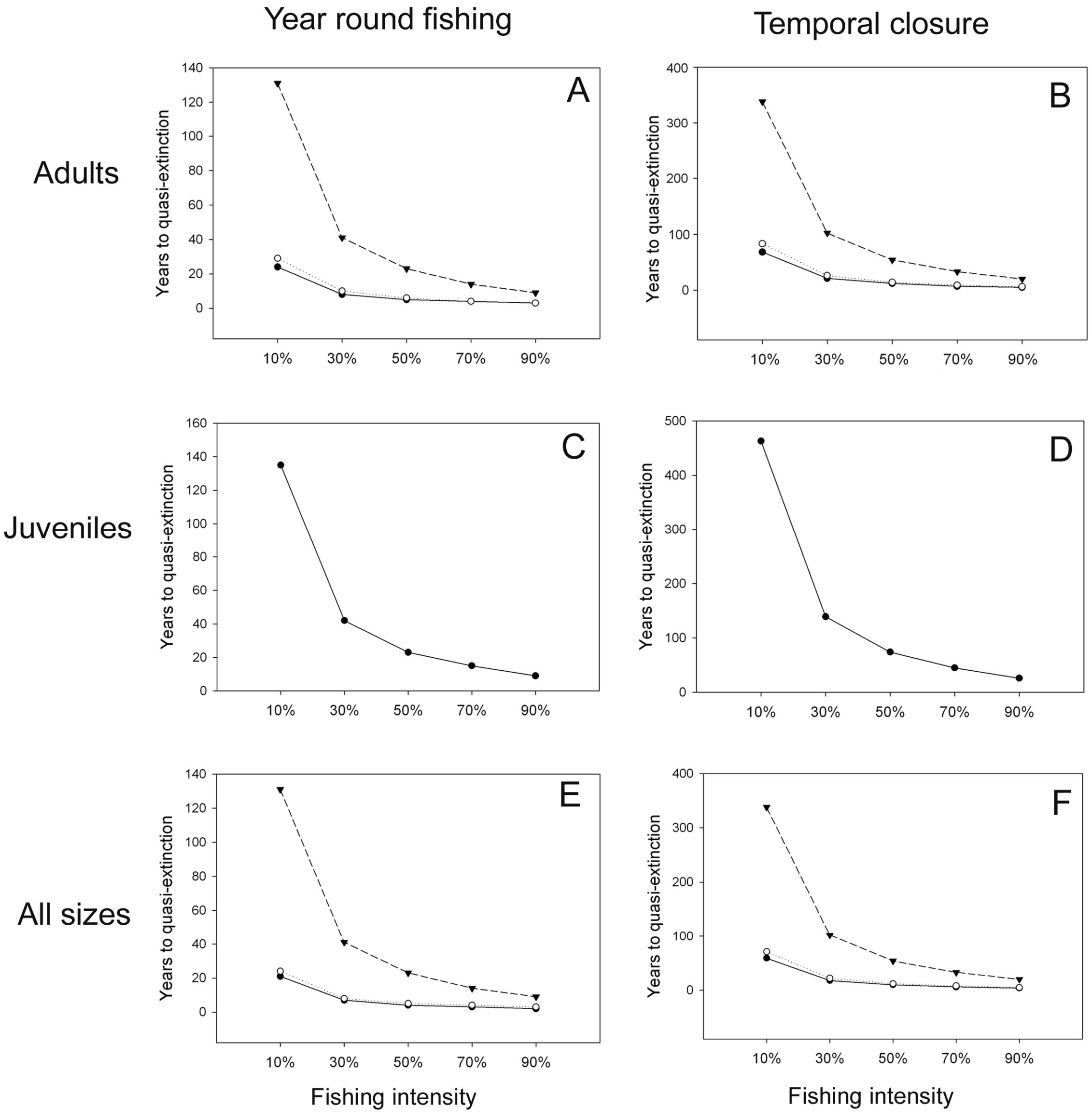

Figure 7. Years to quasi-extinction for seahorse (*Hippocampus comes*) populations in the Danajon Bank, with population growth set to λ = 1. Adults (A, B) or all animals (E, F) were collected under a 10 cm minimum size limit (●), a 14 cm minimum size limit (○) and a 10-14 cm slot size (▼), while all sizes of juveniles were captured equally whether alone (C, D) or with adults (E, F). Population size is modeled at five different monthly fishing intensities, exerted on populations throughout the year (left side, A, C, E) or only during the peak fishing season (right side, B, D, F).

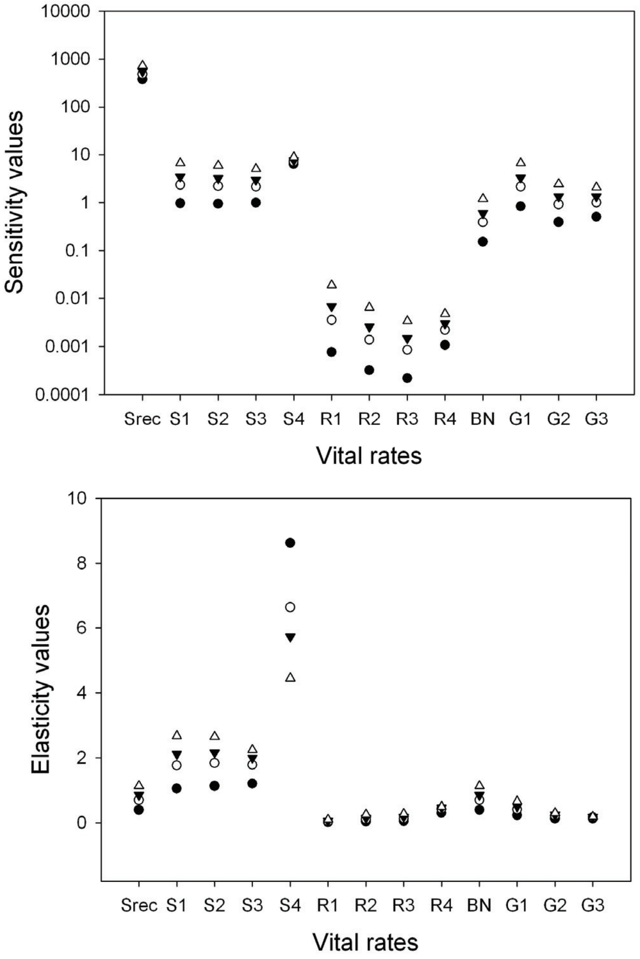

Figure 8. Deterministic sensitivity and elasticity of population growth to values of vital rates used in the base projection matrix for *Hippocampus comes*. Sensitivities and elasticities were explored at growth rates corresponding to stability (λ = 1, Srec = 0.00143,)(○), halved planktonic survivorship (Srec) (λ = 0.692, Srec_low = 0.5*Srec_stable,) (●), in situ population growth (λ = 1.242, Srec = 0.0019) (▼) and doubled planktonic survivorship (λ = 1.863, Srec_high = 2*Srec_stable) (Δ). R = fertility terms, BN = total number of broods, S = survivorship terms, G = growth terms. Numbers following vital rates represent relevant stage classes, where 1 = juveniles, 2 = algal adults, 3 = coral adults and 4 = site faithful adults.

Appendix I

Table 1. Growth transition probabilities for animals moving between or staying within, all size-stages for *Hippocampus comes* from the Danajon Bank, Philippines. Stages are defined in Table 1 in the main text.

Month	**Transition size class, mm (SLc),**			
January	To Juv	To AA	To CA	To SFA
From Juv	0.7694	0.2274	0.0034	0
From AA		0.7469	0.2516	0.0015
From CA			0.7970	02030
From SFA				1.0
February	To Juv	To AA	To CA	To SFA
From Juv	0.7588	0.2386	0.0026	0
From AA		0.7552	0.2439	0.0009
From CA			0.7973	0.2027
From SFA				1.0
March	To Juv	To AA	To CA	To SFA
From Juv	0.7841	0.2136	0.0023	0
From AA		0.7697	0.2296	0.0007
From CA			0.8083	0.1917
From SFA				1.0
April	To Juv	To AA	To CA	To SFA
From Juv	0.8087	0.1887	0.0026	0
From AA		0.7847	0.2145	0.0008
From CA			0.8240	0.1760
From SFA				1.0
May	To Juv	To AA	To CA	To SFA
From Juv	0.8170	0.1810	0.0028	0
From AA		0.7992	0.2049	0.0009
From CA			0.8385	0.1615
From SFA				1.0
June	To Juv	To AA	To CA	To SFA
From Juv	0.8255	0.1717	0.0027	0

From AA		0.7978	0.2012	0.0010
From CA			0.8489	0.1511
From SFA				1.0
July	To Juv	To AA	To CA	To SFA
From Juv	0.8365	0.1607	0.0027	0
From AA		0.7971	0.2016	0.0012
From CA			0.8553	0.1447
From SFA				1.0
August	To Juv	To AA	To CA	To SFA
From Juv	0.8450	0.1522	0.0028	0
From AA		0.7919	0.2066	0.0015
From CA			0.8567	0.1433
From SFA				1.0
September	To Juv	To AA	To CA	To SFA
From Juv	0.8449	0.1522	0.0029	0
From AA		0.7809	0.2174	0.0019
From CA			0.8513	0.1487
From SFA				1.0
October	To Juv	To AA	To CA	To SFA
From Juv	0.8428	0.1542	0.0029	0
From AA		0.7662	0.2317	0.0022
From CA			0.8393	0.1607
From SFA				1.0
November	To Juv	To AA	To CA	To SFA
From Juv	0.8217	0.1749	0.0034	0
From AA		0.7533	0.2444	0.0024
From CA			0.8233	0.1767
From SFA				1.0
December	To Juv	To AA	To CA	To SFA
From Juv	0.8028	0.1941	0.0032	0
From AA		0.7457	0.2525	0.0019
From CA			0.8062	0.1938
From SFA				1.0

Appendix II – Apparent survivorship

From CMR, we estimated apparent survival and probability of recapture via Program Mark 4.3. We generated encounter histories for all marked seahorses from April 2001-2002, using sequences of 1s and 0s to represent re-sightings or absences respectively. We used Cormack Jolly Seber models because data were collected from an open population of live animals that were recaptured then "released" alive (White & Burnham 1999). Animals were visually identified by either collar and/or VIFE tags and 93 observation events were agglomerated into 68 "observation periods", each representing one full examination of the focal grid: no periods were > 14 days.
Before modeling, we used goodness of fit tests (GOF) from program U-CARE to check that the structure of data in our starting (most parameterized) model [Φ(t*s)p(t*s)], met the assumptions underlying the chosen CJS model, particularly that: a) every marked animal at time (i) had the same probability of recapture (pi), and b) that every marked animal immediately after time (i) had the same probability of surviving to time (i+1). GOF tests from program U-CARE are most appropriate when working with sparse cohort-specific contingency tables which arise when new animals are only found infrequently, as we experienced on our regularly observed monitored focal observation grid. Sex (s) and time-specific (t) differences in apparent survival (Φ) and recapture probabilities (p) were investigated among sixteen candidate models that examined combinations of time-invariant [Φ(.)p(.)], time-variant [Φ(t)p(t)], or group-specific survivorship and recapture probability [Φ(s)p(s)]. Models were based on physically mature males and females found on the grid or in the surrounding searched buffer area. These were compared on the basis of the Quasi likelihood adjusted Akaike Information Criteria (QAICc), and selected using rules of thumb given in Cooch and White (http://www.phidot.org/software/mark/docs/book/), that models are well differentiated at QAIC values >7, but not at values <2. Using similar methods, a second set of models were used to examine the effects of size/age and time on survival and recapture, dividing animals into one set of biologically relevant size/classes corresponding to juveniles (< size at maturity, 9.6 cm), small adults (9.6-17.0 cm) and site faithful adults (17.0 cm+). We did not model stages divided by other size boundaries.

Appendix III – Model Assumptions

Vital rate inputs used in this model represent the best available in situ demographic information for tropical seahorses. Nonetheless, they are also values derived from data collected over short temporal and spatial scales. Since demographic models are data intensive, it is common that not all inputs be as robust as desired. In fact, many models are built on demographic rates borrowed from related congeners (Heppell 2007; Slooten et al. 2000; Wielgus et al. 2007). Here our model was parameterized from rates obtained from in situ data, all collected within one population of *H. comes*, with the exception of planktonic survivorship. The latter was modeled over a range of values, which exerted meaningful effects on population growth rates ($\lambda = 0.692\text{-}1.863$). Since survival of very young fishes in blue water is exceedingly difficult to estimate (Letcher et al. 1996), one feasible approach to generating estimates of planktonic survival for marine organisms such as seahorses, may be to back-calculate these values based on strong abundance time-series that give accurate estimates of population growth rates.

Stochasticity was not incorporated into this model because we do not presently have an understanding of inter-annual variation in the vital rates of *H. comes*. Stochastic effects generally decrease population growth rates, relative to deterministic predictions. This means that populations with positive deterministic growth rates could still be at stochastic risk of extinction (Lacy 1993). In typical situations, where data are scarce because of limited sampling duration (< 5 years), or limited sampling intensity, deterministic models may give results that upwardly bias projected population growth, but that have less associated uncertainty than stochastic models: for the purposes of decision-making, more precise estimates with a known bias may be preferable to poor estimates with large uncertainty (Doak et al. 2005).

In order to incorporate more realistic levels of uncertainty in models, it will be necessary to estimate demographic rates, over multiple census years (>5 years has been suggested by Doak et al. 2005). A fresh group of first stage individuals must be marked and followed at each census, along with ongoing marking of larger stages, which will diminish in number via senescence (Morris & Doak 2002). Inter-annual variation in vital rates should also be used to evaluate the reliability of conservation actions identified via elasticity analysis (e.g. using methods such as life stage simulation analysis, Mills et al. 1999; Wisdom et al. 2000).

Density dependence is a pervasive characteristic of biological populations (Brook & Bradshaw 2006). Without any understanding of these processes in *H. comes*, we deliberately avoided constructing hypothetical density-dependent scenarios. This approach assumes that dynamics are not likely to change meaningfully over the range of modeled population densities, in either a compensatory or depensatory manner (Morris & Doak 2002). We presently have no ways of evaluating the validity of this assumption. We acknowledge that persistence and elasticity values would be likely to vary with the inclusion of density dependence.

Meta-analyses from reef fishes tentatively indicate that recruitment is not density dependent, but that mortality is negatively density dependent, and occurs early post-settlement, caused largely by predation (Hixon & Webster 2002). However, both inside no-take marine reserves (recently established, but where predator densities are relatively high) and in fished waters, *H. comes* are found at comparable and similarly low densities (6.11 ± 1.97 individuals m^{-2} X 10^{-4} inside, versus 7.28 ± 1.57 individuals m^{-2} X 10^{-4} outside) (S. K.M., unpublished data). Positive density dependence (allee affects) could theoretically affect seahorse abundance by depressing reproduction should animals have difficulty finding partners (Foster & Vincent 2004). However, most landed males are pregnant (Project Seahorse, unpublished data), suggesting that even at low densities, seahorses are capable of finding mates.

For simplicity, we assumed that animals in the Danajon Bank represent a demographically closed population. Information from Chapter 1 indicates that planktonic young may be moving on the order of 20-200 km, which would keep the great majority of animals within the Danajon Reef system. The philopatry of settled juveniles (Stage 1) is unknown and adult movement (Stages 2-4) appears to be restricted to home ranges <100

m^2 and often smaller (Perante et al. 1998). The proximity of reefs and shallow complex habitat fringing Cebu and Leyte provinces, also known to have populations of *H. comes* (Casey 1999), may be sources of immigrants into the Danajon Bank. However, we have insufficient knowledge of current patterns or abundance in these areas to assume that neighbouring waters are a meaningful source of demographic support for Danajon Bank populations.

OVERALL CONCLUSIONS

> *"Tropical conservation happens in a world of zero-sum games, difficult trade-offs and threats that can irretrievably transform the most biodiverse systems in a matter of days. It is a world where effective conservation, if it happens at all, has to be strategic, seeking to do the maximum possible at the greatest possible scale with resources dwarfed by the scale of the challenge." (Cleary 2006)*

My thesis was largely designed to broaden our general understanding of the ecology, behaviour and demography of teleost fishes, using the unusual morphology of two seahorse species (*Hippocampus comes* and *H. spinosissimus*) to test predictions around life history structure and strategies typically associated with tropical reef fishes. Despite their unique body plan, apparent capacity for immediate settlement and highly specialized parental care, I found that seahorses exhibit ontogenetic ecology largely comparable to most perciform reef fishes in tropical systems. These similarities include: 1) a broadly bipartite life history, comprising a planktonic juvenile phase followed by a less mobile, settled, benthic phase (Leis 1991), 2) dispersal ranging from 20-200 km, comparable to ecologically relevant connectivity on the order of 10-100 km observed in other reef fishes (Cowen et al. 2006), 3) young that advect passively with ocean currents early in the pelagic phase, and 4) ontogenetic habitat associations that functionally divide settled, benthic individuals into multiple ecologically distinct stages (e.g. Cocheret de la Morinière et al. 2003).

Despite conforming to many expectations of reef fishes, tropical seahorses also exhibit distinctive or exceptional traits that can be used to both expand and challenge our current understanding of reef fish ecology. First, although they disperse in the plankton, tropical seahorses have a pelagic phase inferred to last between 5-10 days, among the shortest noted in reef fishes. Second, seahorse young were able to orient to solar cues and exhibited complex burst swimming associated with prey capture during the first days of their planktonic existence; such abilities have not yet been observed in the youngest of other reef fishes. Third, juvenile seahorses were found associated with structurally complex macroalgal beds which are seldom described as nursery grounds in tropical reef ecosystems; most research has focused on the role of seagrass beds and mangroves as refugia and feeding areas for juvenile reef fishes.

I made direct use of my ecological findings (Chapters 1-4) in order to evaluate efforts to manage the genus *Hippocampus* for conservation (Chapter 5). Partly or fully tropical species comprise 70 % of the genus *Hippocampus* and are the principal species in an expanding international trade in these fishes. My research focused primarily on the mid-sized tiger tail seahorse, *H. comes* Cantor 1850 and, secondarily, on sympatric congener *H. spinosissimus* Weber 1913, both found in the central Philippines.

In this discussion, I integrate my work to discuss how my findings bear on seahorses, and then on reef fishes in general. I begin by summarizing the life history of *H. comes* (including my new information from Chapters 1, 2, 3), then infer the vulnerability and recovery potential of *H. comes* populations (Chapters 4, 5). More broadly, I contextualize results as they expand our understanding of bipartite life histories in demersal reef fishes (Chapters 1), the role of behaviour in dispersal (Chapter 2), the implications of stage-based habitat use in reef fishes (Chapters 1, 3, 4) and management of tropical seahorses and other small scale, sedentary, spatially structured reef fisheries (S-fisheries, sensu Orensanz et al. 2005) (Chapter 5).

The Stage-Structured Life History of Tropical Seahorses
(Table 1)

I found that the life cycle of *Hippocampus comes* begins with a short period in the plankton from release (ca. 1.0 cm SLc) to settlement (as small as 2.0-3.0 cm, but probably about 3.0-4.0 cm SLc). During the early pelagic period (I observed only the period from birth to 4 days of age), *H. comes* young exhibit a capacity for complex behaviours that include burst swimming associated with prey capture and orientation relative to solar cues. The ability to orient relative to current develops on a daily basis, but there is no evidence that young can affect their dispersive trajectories in the first days following release; rather they drift passively with current, while feeding. *Hippocampus comes* is believed to spend 5-10 days in the plankton, while *H. spinosissimus* may spend longer, and both species are believe to disperse minimum distances on the order of 10-200 km. I detected no evidence for a relationship between young and floating debris, indicating that rafting is unlikely to play a regular role in dispersal. Research has yet to investigate the transition between open water and the benthos, or pre-settlement behaviours and survivorship associated with this period. Provided otoliths could be recovered from marketed fish and in sufficient numbers, new isotopic methods such as Ba137 injections might be used effectively in this brooding multiple-spawner to mark young for direct tracking (Thorrold et al. 2006).

Settlement is likely to occur year around, commensurate with year round reproduction. However, populations in the Danajon Bank experience an apparent recruitment pulse from February to May, which peaks in March. Growth rates suggest that this corresponds to a surge in either reproductive output or survivorship (or both) when births (releases) are twice those during the rest of the year. This period corresponds to Oct.-Jan., the period of the northeast monsoon in the central Philippines.

After settlement, juvenile (settled, sexually immature) *H. comes* (3.5-9.3 cm) predominate in wild algal beds that are composed mainly of *Sargassum* spp., but also regularly include *Dictyota* spp., *Padina* spp. and *Hypnea* spp. Juveniles are not obligately associated with wild algal beds, but are only half as abundant on coral reefs and one fourth as dense in farmed macroalgal beds. In the Danajon Bank, approximately 70 % of holdfasts used by juveniles are macroalgae, and the remainder are branching sponges. Juveniles also show strong preference for rare substrata that include twine or submerged tree branches. Juveniles exhibit aggregation with conspecifics and sub-adults are sometimes found paired. It is possible that juveniles migrate on small spatial scales (<100 m) out of algal beds into adjoining adjoin coral crest zones as they mature: the timing of this transition may be driven by seasonal fragmentation of *Sargassum* spp. thalli when water temperatures increase following the Northeast monsoon (S.K.M., unpublished data). Further research is required to understand juvenile diet and scales of movement.

Adult (>11.6 cm) *Hippocampus comes* are found in both coral and algal communities, although the largest individuals are on coral reefs. Holdfasts used at sizes >13.5 cm include diverse biogenic structures such as branching sponges (*Clathria* spp.), branching corals (*Porites* spp., *Montipora* spp.) and tall strap-like seagrass (*Enhalus acoroides*). These holdfasts are often large or rare relative to surrounding matrix communities. Adults are aggregated, usually in pairs, although threesomes or quadruples are seen less frequently (Perante et al. 2002). Although *H. comes* has been described as nocturnal (Perante et al. 2002) because it rises up on holdfasts at night, animals are usually immobile during this period. Rather, I observed them actively swimming either to holdfasts, or back into reef structure during crepuscular periods. My underwater footage of in situ, caged subjects confirms these activity patterns and that *H. comes* does not feed at night, but does exhibit snapping and striking during crepuscular and daylight hours (S.K.M., unpublished data). Unlike other seahorses, reproductive behaviours such as greeting, brightening and promenading (Vincent & Sadler 1995) have not been observed in *H. comes*. Release of young usually occurs at night (S.K.M., unpublished data).

Inherent Vulnerability, Fishing Impacts and Recovery Potential (Table 2).

A plethora of criteria have been designed to evaluate susceptibility to extinction (Roberts & Hawkins 1999), vulnerability to exploitation (Stobutzki et al. 2001) and the relative health of fisheries (Anon 2004). Here I used criteria from diverse sources to assess what factors might confer risk or resilence for *H. comes*. Rather than vital rates, it is aspects of behaviour, susceptibility to fishing, distribution (range and abundance), and (absent) management that increase the inherent vulnerability of this tropical seahorse. *Hippocampus comes* shows moderate potential for recovery following depletion.

Most of the physical rates that govern population turnover of *H. comes* confer low susceptibility to risk (Roberts & Hawkins 1999) (Table 2) and are consistent with species with opportunistic life histories. This small fish grows rapidly, matures young, reproduces frequently throughout the year and is probably short-lived (Chapter 4). Vital rates exhibited by *H. comes* are quantitatively comparable to other tropical syngnathids (Chapter 4) and qualitatively similar to its temperate congener *H. guttulatus*. Relative to the latter, growth is more rapid and longevity is probably shorter (Curtis & Vincent 2006). Since metabolic rate is directly related to temperature, these differences are consistent with general differences seen between temperate and tropical fishes (Pauly 1998). Furthermore, opportunistic demography predicts that if refugia are available, species can be resilient to frequent and intense disturbance (Winemiller 2005). In the Danajon Bank, *H. comes* thrive in shallow waters that experience high natural disturbance via tidal variation in water temperature, turbidity and depth along with frequent exposure to typhoons.

A number of behaviours exhibited by *H. comes* increase its vulnerability, particularly in fished systems. Reproductive behaviours that include parental care and monogamy decrease reproductive output relative to species without these traits and are characteristics common to fishes with equilibrium life history strategies (reviewed in Foster & Vincent 2004). Parental care reduces the chance of successful reproduction prior to capture (Stobutzki et al. 2001), while fishing monogamous species disrupts pair bonds and arrests reproduction after the loss of a mate (Vincent & Sadovy 1998). Furthermore, most fishers understand that seahorses are paired, site-faithful, and occupy small home ranges, so undertake intense searches for both animals in a pair, once the first is captured. Reduced mating success via depensation (allee effects) is theoretically possible in heavily fished systems. However, in the Danajon Bank, most large landed males (>120mm) (Chapter 4) were brooding, suggesting that current conditions are not compromising animals' ability to find partners. Non-reproductive behaviours such as the propensity to rise up on holdfasts at night (distinctive in *H. comes*, among studied species) might also increase susceptibility to capture. At night, animals seldom exhibit flight behaviour seen during active crepuscular periods (S. Morgan, pers. obs.).

The limited geographic range and restricted habitat use exhibited by *H. comes* also increase its inherent vulnerability. The species is restricted to the South China Sea, with most sightings from within the Philippines (Lourie et al. 2004), where suitable shallow-water habitat is vulnerable to destructive activities such as blast-fishing, trampling, boat damage along with shoreline degradation and land-based nutrient and sediment outputs. *Hippocampus comes* appears to be exclusively demersal and associated with structurally complex habitat (except during planktonic dispersal), so is found only in narrow horizontal and vertical strata fringing shorelines. This makes it easily accessible to fishers without the need for costly gear. *Hippocampus comes* as well as other seahorse species, show strong preference for distinctive or artificial structures (Foster & Vincent 2004), which can also be targeted by fishers. Large animals are particularly vulnerable because their preferred holdfasts provide poor camouflage relative to foliose algal environments used by juveniles (Morgan & Vincent 2007).

Targeted seahorse fishing, in which fishers capture animals while breath-hold diving, is largely benign from an ecosystem perspective (Table 2). When seahorses are hand-harvested, there is little to no gear impact on habitat. Furthermore, tropical food webs are speciose, but with few individuals of any given species in most communities. Seahorses are among hundreds of fish species on reefs in the Philippines and there is presently no strong evidence that seahorses play a sufficiently substantial role in the trophic structure of tropical foodwebs that their removal is likely to shift systems to alternative stable states (for examples to the otherwise, see Worm & Myers 2003). There may be greater potential for community/ecosystem effects where seahorses are found at much higher densities (Curtis 2004), such as in some temperate systems (although most such populations are not presently targeted by fisheries).

Some traits of *H. comes* suggest strong potential for recovery following exploitation while others do not (Table 2): how these factors interact to govern persistence in *H. comes* remains unknown. Traits such as a short pelagic phase (Chapter 2), restricted adult movement (Perante et al. 2002, S.K.M., unpublished data,) and already documented declines (A. Maypa, unpublished data in Morgan & Lourie 2006) decrease the likelihood of recovery (Hutchings 2001b; Roberts & Hawkins 1999). Furthermore, in the Danajon Bank, blast-fishing for food fishes causes extensive damage to biogenic cover (Marcus et al. 2007; Saila et al. 1993), and reduces the structural complexity of habitat used by adults. The habitat of the juvenile phase is also threatened by expanding mariculture which replaces wild algal beds with farmed species (Morgan & Vincent 2007; Zemke-White & Flores 2001).

Seahorse fisheries in the Philippines rate poorly on almost any commercial management metric (Anon 2004): in best cases there is limited monitoring and research as well as disaggregated use of marine protected areas. However, there are no regular stock assessments, no use of scientific advice to guide the harvesting that does occur, and no fisheries regulations that are nationally enforced (although CITES obligations appear in the Philippines Fisheries Code).

The Ubiquity of a Bipartite Life History and Dispersal Among Reef Fishes

My findings strengthen the assumption that bipartite life histories are ubiquitous among most reef fish families. Bipartite life histories are common to >95 % of demersal reef fish famillies (Leis 1991) which are first planktonic as larvae or small juveniles and then take up a sedentary benthic existence as adults. Relatively little is understood about the planktonic phase of most reef fish life histories. They are difficult to study because subjects are usually very small, found at low densities in three dimensional habitats, experience high natural mortality and can be difficult to identify. My research showed that *H. comes* and *H. spinosissimus* both experience a planktonic phase like most other reef fishes. Indeed, present evidence suggests that a bipartite life history may be conserved across the genus *Hippocampus,* although planktonic densities vary (Chapter 1). Only one report, from ex situ observation, suggested that a Mediterranean species (*H. fuscus)* settled immediately, by grasping tank furnishing immediately after release (Golani & Fine 2002). My results also indicate that bipartite reef fish life histories persist despite morphological and behavioural traits apparently ill-suited to a planktonic phase or enabling immediate settlement (e.g. heavy pigmentation, young metamorphosed upon release, and the ability to grasp structure with prehensile tails within hours after release). My findings also suggest that ex situ observations of immediate settlement (e.g. in *H. fuscus*) may not be representative of wild behaviour with respect to planktonic dispersal.

My research suggests that tropical seahorses may exhibit amongst the shortest pelagic periods yet inferred for coral reef fishes. In fact, their planktonic phase of 5-10 days most resembles sessile or low motility invertebrates which often disperse over periods of 8-10 days (Bonhomme & Planes 2000), versus 20-30 as per most reef fishes (Sale & Kritzer 2003). Along with some damselfishes (Pomacentridae) which can have pelagic stages as short as a week (Thresher et al. 1989), the Panda Clownfish, *Amphiprion polymnus,* is rare in having a pelagic phase of comparable length (9-12 days in situ) to *H. comes* (Jones et al. 2005).

My observations are consistent with theory suggesting that the arrangement of suitable habitat in space (seascape) may be an important influence on the evolution of dispersal periods (Dytham 2003). The presence of an unusually short planktonic phases in tropical seahorses, some damselfishes (Bay et al. 2006) and the Panda Clownfish (Jones et al. 2005) is most consistent with theory predicting shorter pelagic periods when settlement habitat is found at low density or is disaggregated (Dytham & Simpson 2007). For example, *Amphiprion polymnus* is an obligate mutualist with large benthic sea anemones which are often found at intervals of >10 km (Jones et al. 2005). Similarly, *H. comes* has a shorter minimum dispersal period than *H. spinosissimus* (as well as a more limited geographic distribution), where the former occupies structurally complex shallow habitats that are rarer than the open sandy/silty expanses between islands (with occasional structure) preferred by the latter. In contrast, seahorses such as *H. abdominalis* and *H. guttulatus* that disperse along continuous coastlines with frequent opportunities for settlement, appear to have a substantially longer dispersive period of 2-3 months (Boisseau 1967; Curtis & Vincent 2006) than either of the tropical archipelago-system species researched here. This is notable, particularly when similar dispersal periods are observed among phylogenetically disparate taxa with different body forms (e.g.

perciform clown fishes vs upright seahorses), and when different dispersal periods are observed within phylogenetically proximate taxa, with similar morphology (e.g. among seahorse species). It could be useful to examine how seascape, physiological and behavioural capacity interact, and whether these factors together can be used to predict planktonic duration amongst diverse taxa of marine fishes.

The short planktonic phase of seahorses is consistent with recent research showing that at least some proportion of reef fish populations may be less "open" than previously thought (Cowen et al. 2000; Jones et al. 2005; Mora & Sale 2002). Limited dispersal distances of 20-200 km for tropical seahorses imply that seahorse young born on the Danajon Bank may also settle in the system. Previous genetic work concurs that tropical seahorses are dispersal-limited over ecological and evolutionary time-scales (Lourie 2004). Similarly, ecologically relevant scales of dispersal for other marine reef fish larvae are thought to occur on the scale of 10 to 100 km (Cowen et al. 2006). These findings have important implications for the connectivity of reefs and archipelagos, where patch populations on immediate spatial scales could receive meaningful demographic support from neighbouring upstream patches, as well as occasional long distance dispersers that will influence genetic diversity, from patches further afield (Mora & Sale 2002). This form of connectivity means that communities with marine reserves could see the outcomes of their conservation actions through replenishment of local fishing grounds by larval exports from protected sites. Furthermore, this scale of dispersal increases incentives for local and regional networks of fishers to manage home fisheries responsibly, for their own livelihood benefits.

Implications of Planktonic Behaviour

My work is among the first studies that show that coral reef fishes have the ability to exhibit complex behaviours early in the pelagic phase, well in advance of settlement. Simulation studies have amply demonstrated that settlement patterns vary substantially based on the inclusion or exclusion of larval behaviour when modeling dispersal and connectivity (Armsworth & Bode 1999). However, ethological research on reef fish young has focused nearly exclusively on the abilities of pre-settlement stage individuals (but see Leis et al. 2007), at the end of their planktonic phase (reviewed in Leis & McCormick 2002). In contrast, Chapter 2 of this thesis examined how behaviour developed in seahorse young during the first days after release, at the beginning of the pelagic phase. One other study has examined the early planktonic behaviour of a reef fish and showed that the pomacentrid damselfish, *Amblyglyphidodon curacao*, has swimming, orientation and vertical positioning capabilities that could influence dispersal outcomes (but did not explicitly address ontogenetic changes) (Leis et al. 2007). Here, we saw that newborn *H. comes* did not have the capacity to swim against ambient currents, seen in many perciform reef fishes, particularly prior to settlement (Fisher 2005), but they did exhibit complex behaviours relative to prey items and solar cues, and their ability to orient relative to ambient currents increased with age. Since seahorses develop directly inside male pouches, they are advanced relative to many reef fish young (e.g. gametes released into the water column) in the early part of their planktonic phase. Similar research is now needed across diverse taxa of fishes to understand how behaviour develops throughout the planktonic phase (Leis et al. 2006) and how this may vary with taxonomy, geography or other factors. Incorporating this biological realism into oceanographic circulation models will be necessary for predicting demographic connectivity among marine populations and networks of protected areas (Cowen et al. 2006).

Implications for Stage-Based Habitat Use in Reef Fishes

My discovery that juveniles use algal beds suggests the need for greater systematic study of how diverse shallow-water communities in the tropics support the sub-adult phases of reef fishes. While most research in warm-water reef ecosystems has focused on the importance of mangrove and seagrass beds to the intermediate juvenile phase of life histories (Mumby et al. 2004; Nagelkerken et al. 2001), my findings support the assertion from temperate systems, that juvenile demersal fishes could associate with diverse environments united by the presence of complex structure that provide appropriate prey or refugia from predation (Heck et al. 2003). Juvenile *H. comes* predominate in wild macroalgal beds that are a natural part of the zonation of tropical reef ecosystems, but have received little systematic attention as nursery habitat (but see Rossier & Kulbicki 2000). Recent research has also shown that the young of other commercially important tropical species such as groupers occupy macroalgal beds (Dahlgren & Eggleston 2001; Jenkins & Wheatley 1998; Light & Jones 1997).

When different life stages occupy distinct communities within reef ecosystems, all of these areas will require protection in order to conserve ontogenetic pathways of connectivity throughout life histories. The data-depauperate nature of most reef fisheries means that little is known about the juvenile habitat requirements of many, if not most, exploited reef organisms. Therefore, anthropogenic activities that disturb natural habitat may have serious consequences for as yet unstudied life stages and the sustainability of reef fisheries. Such effects have only recently been observed in temperate systems, where bottom trawling has destroyed epifaunal communities of deep-water corals and sponges needed by the juvenile phase of demersal fishes such as cod (Collie et al. 1997). Marine planning processes in tropical systems, which presently provide principle protection to coral crest communities, would likely benefit from incorporating ontogenetic needs in spatial management. In the absence of comprehensive life history information, preserving representative sub-sections of the natural community diversity of reef ecosystems could be a precautionary approach.

Research and Management Approaches with Utility to S-fisheries

My thesis research made direct use of ontogenetic, demographic information to examine alternative management scenarios for seahorse fisheries. Seahorses are one example of "S" fisheries: fishing that occurs on small scales and captures sedentary, spatially-structured benthic organisms (sensu Orensanz et al. 2005). Most of these fisheries are both data and resource limited, so are rarely managed. Simultaneously, they are important sources of protein and/or livelihoods (Castilla & Defeo 2005) and need for their resources, particularly in developing countries, is expected to increase (Newton et al. 2007).

In order to address the ontogenetic ecology and conservation of tropical seahorses, I required methods that could address data gaps that existed at most stages in the life history. For data-limited systems, crude demographic rates for all life stages may be of greater use than refined information on a few life stages, with a complete dearth of data on others. Methods to acquire information about life histories and demography rapidly and inexpensively already exist, and could be used more extensively. For example, pilot studies and rapid assessment (Hodgson 2000; Kramer et al. 2005; Pitcher 1999) can be optimized by consulting the local ecological knowledge (sensu Ruddle 1994) of fishers or by using their fishing skills to locate research subjects (e.g. Chapter 3). Business interests such as commercial aquaculture facilities may also possess advanced understandings of species' life histories and ontogenetic requirements (e.g. Chapter 2). When life stages have not been researched or cannot be found, demographic rates can be borrowed from related taxa, or assumed from empirical relationships among congeners (Finkelstein et al. 2007; Frisk et al. 2001; Weilgus et al. 2007) (Chapter 5). If these data are unavailable or unsuitable, meta-analyses from a suite of unrelated taxa that experience similar environmental and physiological constraints can be used to obtain or confirm parameters of interest (e.g. Foster & Vincent 2005; Froese & Binohlan 2000; Froese & Binohlan 2003) (Chapters 1, 4). These approaches are increasingly possible with online access to internet databases such as FishBase, www.fishbase.org. When working with taxa that are data-limited but previously researched, information can often be mined from diverse sources or consolidated in useful ways (e.g. Chapter 4). Where data are not congruent or span a range of values, *a priori* modeling can help researchers to make explicit their assumptions, perform gap analyses, quantify uncertainty and prioritize next steps for management-reform (Chapter 5). Quantitative analyses can also be undertaken for little cost relative to in situ monitoring, but will never be a useful substitute for field data.

Finding methods to manage data-limited artisanal reef fisheries may require drawing on best practices from other types of fisheries, as well as fundamentally novel methods, suited particularly to reef assemblages. When resources are available for management, incentive-based approaches (Grafton et al. 2006) that may be useful for reef fisheries include rights-based fishing (dedicated access privileges sensu U.S. Commission on Ocean Policy) which could range from traditional (tenurial rights/customary sea tenure, territorial user rights (TURFs)) to commercial quota-based approaches such as individually transferable quotas (ITQs) to hybridized intermediates such as cooperatives or use of co-management in combination with traditional tenure (e.g. Cook Islands *Trochus* fishery Adams 1998). These methods could be used alone or with approaches such as participatory forms of spatial management (Hilborn et al. 2004). New management frameworks such as traffic light approaches that have been specifically designed for use in data-poor situations may also be necessary when managers have limited experience modeling population dynamics and are without access to time series on stock and recruitment (Caddy 2002).

In this thesis, I used population viability analysis (PVA) as one analytical method to investigate a suite of possible management options for seahorses in a reef ecosystem. This approach is a valuable tool for assessing targeted, selective reef fisheries such as seahorse fishing, but may be limited in its application to reef fisheries captured as multi-species assemblages. PVA is a fundamentally single species approach and, although it can be extended to multiple species (Akcakaya 2000), it would likely be prohibitively expensive or data-intensive to implement in any practical way for reef organisms that are captured collectively or non-selectively via methods such as blast-fishing or trawling. In these situations, scientific assessment may not be feasible, affordable or timely, so pragmatic efforts such as community-based marine protected areas may be among the best options for communities to secure and protect resources (Hilborn et al. 2004).

In many cases, single species approaches to assessment will also remain pragmatic and an important part of managing reef fisheries. In these situations, PVA will be useful, even when demographic inputs are limited, to prioritize among management options and to model selectively targeted species. Hand-gathered, gleaned, spear-fished, or individual hook and line captured resources such as seahorses, urchins, sand dollars, shells, corals, aquarium fishes, cuttlefish, sea cucumbers and particular fin fishes are examples of target species that could benefit from the application of PVA. Theoretically, demographically rigorous PVA could be feasible for selective, high-value fisheries such as the live reef fish trade, if these fisheries were managed scientifically. In data-limited situations, assessing the viability of flagship species such as seahorses could also be used to incite management action and to provide umbrella protection (e.g. spatial closures) for sympatric organisms, unlikely to be managed based on their own demography.

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Table 1. Summary of information obtained on various aspects of the life history and ecology of *Hippocampus comes* (and *H. spinosissimus*) during the course of dissertation research, as well as outstanding research questions. Contributions marked with an asterix (*) indicate unpublished analyses, not present in the thesis. Contributions marked with a cross symbol (†) indicate data that has been researched elsewhere, with given citation. Priority research questions are given in bold.

	Tropical juveniles (planktonic and settled)		**Tropical adults**	
	Research contributions	**Outstanding research questions**	**Research contributions**	**Outstanding research questions**
Dispersal/ movement	● Short pelagic phase (*H. comes* 5-10 days, *H. spinosissimus* 8-10 days) ● *H. comes* and *H. spinosissimus* are believed to disperse distances of 12-210 km ● Capable of complex behaviour within the first 4 days after birth, including active orientation relative to prey items and solar cues ● Advected passively and no evidence of effective swimming against ambient currents	● **Direct validation of the length of the planktonic phase for *H. comes* and other tropical seahorses** ● Understand seasonal variation in the abundance of planktonic young ● Understand the influence of behaviour on dispersal trajectories throughout the planktonic phase, particularly prior to settlement ● Understand movement of settled juveniles.	● *H. comes* adults have small home ranges, with mean area of occurrence = 133.4 m^2 and mean area of occupancy = 22.7 m^2 (sensu IUCN 2001) * † Perante et al. 2002	● Understand the effects of habitat and disturbance on movement ● Quantify the frequency, magnitude and sexual dimorphism (if any), of adult migration outside of home ranges ● Investigate the frequency of home range relocation ● Investigate why *H. comes* move to the top of holdfasts at night (increases susceptibility to fishing mortality)
Habitat Use	● Predominate in wild algal beds ● Mainly use algal and sponge holdfasts that are not distinct from the surrounding matrix ● Exhibit strong preference for rare substrata such as twine and submerged tree branches.	● Investigate mechanisms governing ontogenetic shifts in habitat use ● Develop predictive and spatially-explicit habitat models to facilitate conservation planning	● Largest most fecund adults are located in benthic areas with high morpho-taxonomic richness (sensu English et al. 1997) ● Most abundant on coral reefs and in wild algal beds ● Large animals (> 135mm) use a diverse assortment of holdfasts, usually large or distinct from he surrounding matrix	● **Quantify habitat use and densities of other tropical seahorse species** ● **Quantify the effects of habitat disturbance on abundance** ● **Understand the diet and trophic ecology** ● Develop predictive spatially-explicit habitat models to facilitate conservation planning
Growth	● Rapid (K = 2.9), with a “square” growth curve exhibiting rapid rise to mean Linf (= 16.7 cm)	● **Confirm in situ growth rates of animals 40-100 mm and species-wide variance in growth rates (over large spatial scales and by habitat)**	● Rapid growth (K = 2.9), with a “square” growth curve exhibiting rapid rise to mean Linf (= 16.7 cm)	● **Quantify population growth rate (λ) and the magnitude of fluctuations in abundance via annual longterm monitoring**

		● Examine with larger sample sizes, whether juveniles growth is best modeled separately from adult growth ● Understand mechanisms regulating differences in juvenile growth (e.g. diet, sex)		● **Quantify species-wide variance in growth rates (over large spatial scales and by habitat)** ● Understand mechanisms regulating differences in individual adult growth (e.g. diet, sex, reproduction)
Reproduction	● length at maturity = 9.3 cm ● Independent validation of an apparent recruitment pulse from Feb-May via underwater visual census	● For *H. comes*, investigate the relationship between seasonal dynamics of wild algal beds and seahorse recruitment	● length at reproduction = 11.6 cm ● Back calculated increase in reproductive output/survivorship corresponding to Northeast monsoon window from Oct-Jan.	● **Assess the effects of population density on reproduction** ● **Assess the effect of season on the proportion of animals reproducing, brood size and brood duration.** ● Describe in situ reproductive behaviour of *H. co*mes
Survival	● Survival of young in planktonic phase (Srec), estimated for *H. comes* based on other demographic rates at less than 1 % annually (0.0014) ● Annual survival of juveniles = 3.5 %	● **Understanding whether survivorship or reproductive output drives the annual recruitment pulse in *H. comes*** ● Understand the influence of density dependence on survival ● Improve our understanding of planktonic survivorship ● Improve estimates of natural and fishing mortality.	● Annual survivorship of mid-sized adults (9.3-17 cm) = 10.4 % ● Annual survivorship of largest adults (>17 cm) = 45.3 % ● Longevity = 2.5+ years	● **Quantify fishing intensity** ● **Quantify longevity in situ** ● Understand the influence of density dependence on survival ● Quantify species-wide variation in adult survival (over large geographical scale and among habitats) ● Improve estimates of natural and of fishing mortality.

Table 2. Summary table giving life history, fisheries and management characteristics for *Hippocampus comes* on the Danajon Bank, Philippines and how these confer risk. Criteria are taken from Curtis (2004), Denney et al. (2002), Hutchings (2001), Jennings et al. (1999), Monterey Bay Seafood Watch capture fisheries evaluations (Anon 2004), Roberts & Hawkins (1999), Stobutzki et al. (2001), and Vincent & Sadovy (1998). Risk is given as a low-intermediate (Int.)-high ranking for Monterey Bay Aquarium Seafood Watch criteria which have quantifiable cut-offs, and as high or low when using criteria defined by Roberts & Hawkins (1999). Otherwise, risk is ranked subjectively relative to other teleosts/seahorses as "greater" or "lower". Criteria definitions from literature sources are given first in the Rationale column, followed by italicized comments that qualify the application of the criteria to *H. comes*.

Risk Criteria	Symbol	Value	Risk conferred	Rationale	Reference
Inherent vulnerability					MBA (2004)
Physical attributes - growth					
Maximum size (mean)	$Linf_{mean}$	16.7 cm	Lower	High rates of recruitment are significantly associated with small body size. *Small maximum (mean) size (Chapter 4)*	Denney et al. (2002), Jennings et al. (1999)
Maximum size (absolute, observed)	$Linf_{abs}$	25.8 cm	Lower	High rates of recruitment are significantly associated with small body size. *Small maximum (absolute) size (Project Seahorse, unpublished data)*	Denney et al. (2002), Jennings et al. (1999)
Maximum age	tmax	2.5 + yr	Low*	<11 years. *But species with short lifespans may also be vulnerable to prolonged periods with poor recruitment (King & McFarlane 2003) *Low tmax (Chapter 4)*	MBA (2004)
Von Bertalanffy growth coefficient	K	2.9 yr^{-1}	Low	>0.16 *Yes (Chapter 4)*	MBA (2004) Denney et al. (2002)
Physical attributes - reproduction					
Age/size at maturity	tm Lm	3.8 months 9.3 cm	Low	< 5 years. Reproduces old or large vs young or small. *Matures young /at small sizes (Chapter 4)*	MBA (2004) Denney et al. (2002) Roberts & Hawkins (1999)
Age/size at reproduction	tr Lr	5.4 months 11.6 cm	Low	Reproduces old or large vs young or small. *Reproduces young/at small sizes (Chapter 4)*	Roberts & Hawkins (1999)
Reproductive frequency	X±sd	21.7 broods yr^{-1} ± 1.26	Low	Semelparity vs. iteroparity. *Iteroparous (Chapter 4)*	Roberts & Hawkins (1999)

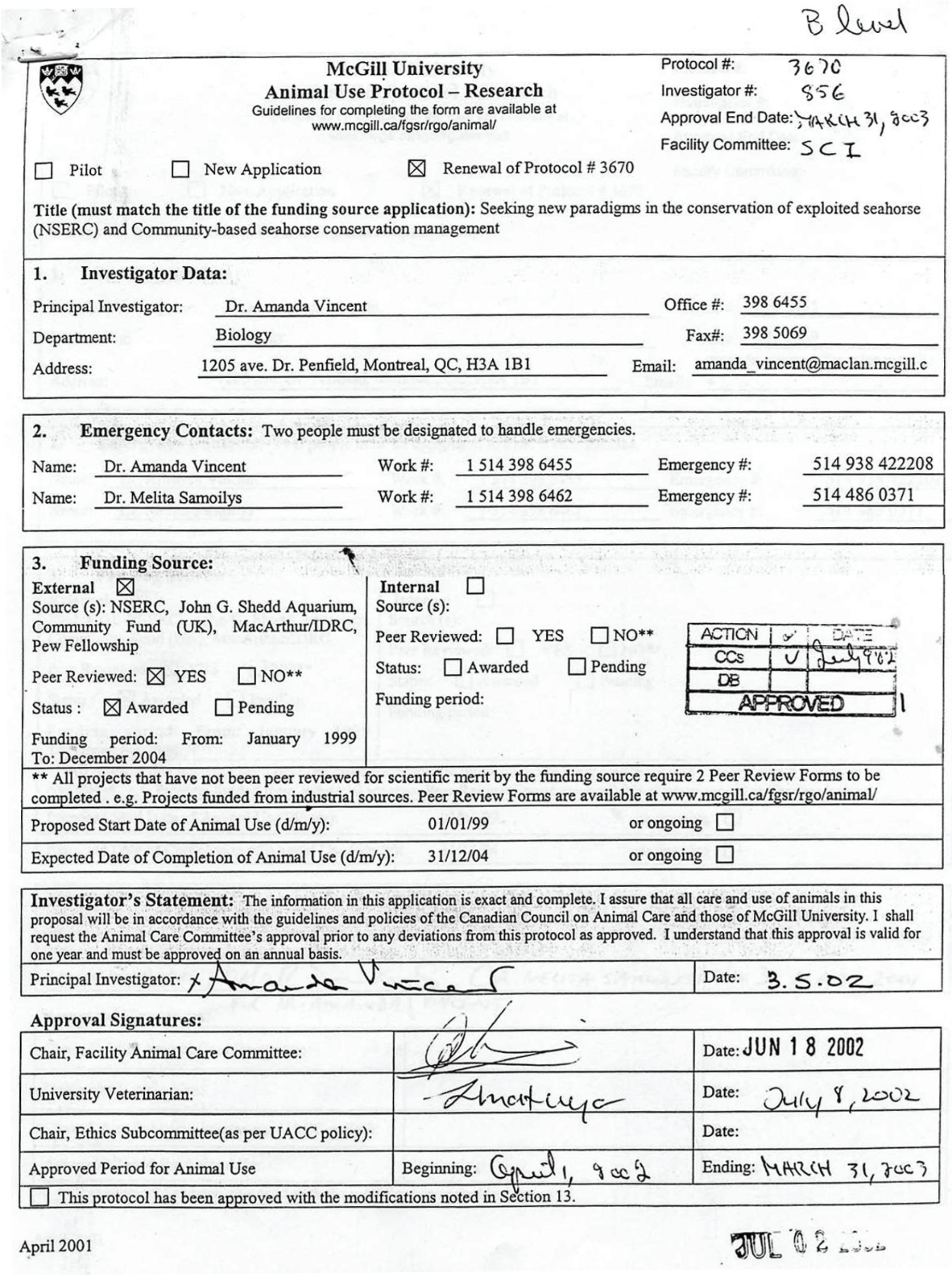
Reproductive potential (fecundity)	X±sd	388 ind. ±172 (Morgan & Lourie 2006)	Low*	>100 ind. yr^{-1} *High output (Chapter 4)*	MBA (2004) * but see (Denney et al. 2002)
Sexual dimorphism			Low	Large vs. small difference in size of sexes. *Not sexually size dimorphic (Chapter 3)*	Roberts & Hawkins (1999)
Physical attributes - survival					
Natural mortality	M_{adult}	1.83	Low*	Low vs. high. **Varies by size, vulnerability may be size-specific (Chapter 4)*	Roberts & Hawkins (1999)
Fishing mortality	F	2.53			
Behaviour					
Mating pattern			Greater	Monogamy vs. polygamy. *Socially and likely sexually, monogamous for one reproductive season and perhaps longer (Perante et al. 2002). Loss of a mate may reduce reproductive rate.*	Vincent & Sadovy (1998)
Parental care			Greater	Bear live young or brood young. *True (Foster & Vincent 2004a)*	Stobutzki (2001)
Spawning aggregations			Low	In aggregations at predictable locations. *Does not form pelagic spawning aggregations.*	Roberts & Hawkins (1999)Vincent & Sadovy (1998)
Sex change			Low	Sex-changing occurs (protandry in particular). *No*	Roberts & Hawkins (1999)Vincent & Sadovy (1998)
Allee effects			Low	Strong allee effects. *Not known, but unlikely at present densities where most males >120 cm are brooding. (Project Seahorse, unpublished data)*	Roberts & Hawkins (1999)
Existence of special behaviours that increase ease or population consequences of capture (migratory bottlenecks, spawning aggregations, site fidelity, unusual attraction to gear, sequential hermaphrodites, segregation by sex OR specific and limited habitat requirements within the species' range)			Int.	Exhibits some behaviours or requirements (1-2) *High site fidelity in adults and limited habitat requirements within the species' range (Perante et al. 2002).*	MBA (2004)
Range, distribution and abundance					
Range			Int.	Occurs in a single ocean basin. *Western Pacific (Lourie et al. 2004)*	MBA (2004)
Depth			Greater	Most of depth distribution susceptible to fishing *Subtidal-20m (Kuiter 2000; Lourie et al. 2004)*	Modified based on Stobutzki (2001)
Demersal vs. pelagic (vertical depth distribution)			High	Narrow or broad vertical depth distribution. *Demersal and occurs in narrow horizontal distributions around atolls. (Chapter 3)*	Roberts & Hawkins (1999) Stobutzki (2001)
Degradation of habitat from non-fishery impacts			High	Habitat has been substantially compromised from non-	MBA (2004)

		fishery impacts and thus has reduced capacity to support this species. *Blast fishing (Marcus et al. 2007), boat damage, trampling, kelp-harvest and mariculture of Eucheuma* spp. *and Kappaphycus* spp. *Not documented whether habitat degradation has decreased densities of H. comes*	
Commonness or rarity	High	Rare vs. abundant. *Mean densities of 1.43 X* 10^{-3} *ind* m^{-2}. *Rare relative to other seahorse species and historic densities. (Chapter 3)*	Roberts & Hawkins (1999)
Habitat vulnerable to destruction by people	Unknown	High vs. low vulnerability. *Blast-fishing regularly practiced in the Danajon Bank, which causes substantial damage to coral structure (Marcus et al. 2007), and in other systems has caused phase shifts to algal communities. Effects in the Danajon Bank unknown since adult H. comes use coral reef and juveniles use algal beds.*	Roberts & Hawkins (1999)
Susceptibility to capture			
Attracted to gear	Greater	Attracted vs. not attracted to fishing gear. *Seahorses (Foster & Vincent 2004a) including H. comes, are attracted to structure and particularly artificial structure (Chapter 3) . This facilitates capture, although they are not attracted to gears specifically for fishing.*	Stobutzki (2001)
Catchability	Unknown	Unknown	Curtis (2004)
Survival during discard	n/a	High vs. low survival during discard. *Survival likely to be high based on observation of fished H. comes and survival of H. erectus in bycatch (Baum et al. 2003a).*	Curtis (2004)
Ability to recover			
Intrinsic rate of increase (r)	Unknown	*Unknown*	MBA (2004)
Compensatory dynamics	Unknown	Compensatory dynamics do or do not exist. *Unknown, life history strategy consistent with opportunistic species (do not show compensation) and equilibrium strategists (do show compensation)(Winemiller 2005).*	Curtis (2004)
Mortality index (L_{infabs}-$L_{meancap}$/$L_{meancap}$-$L_{minfished}$)	Greater	Mortality Index >1.88 *For H. comes* ((25.9-14.5)/(14.5-5.2)) = 2.06	Modified from Stobutzki (2001)
Dispersal	High	Short distance vs. long distance dispersal. *Predicted dispersal distances ranging from 12-210 km. (Chapter 2)*	Roberts & Hawkins (1999)
Adult movement	High	Low vs. high mobility. *Low, small home ranges. Mean area of occupancy = 22.7* $m^{2,}$ *mean area of occurrence = 133.4*m^2 *(sensu IUCN 2001)* *(S.K.M., unpublished data)*	Roberts & Hawkins (1999)
Magnitude of population decline (relative to size of future population)	Greater	Population declines are correlated with time to recovery. *Populations of H. comes in the central Philippines have*	Hutchings (2001)

		experienced multiple local declines of 65-100 % (A. Maypa, unpublished data)	
Ability to colonise (see dispersal and adult movement above)	Low	Good vs. poor colonizing ability. *Possess many characteristics of species with opportunisitic life histories, generally believed to have strong colonization potential (Winemiller 2005).*	Roberts & Hawkins (1999)
Competitive ability	Unknown	Poor vs. good competitive ability. *Unknown*	Roberts & Hawkins (1999)
Probability of breeding before capture	Lower	High vs. low probability of breeding before capture. *Most size classes in catch are reproductive. Mean size of captures = 14.52 cm, (n = 11 928), size at first capture 5.20 cm, proportion of total catch < Lm = 0.07, proportion of total catch <Lr = 0.17*	Stobutzki (2001)
Removal rate	Unknown	Proportion removed by fishing. *Unknown*	Stobutzki (2001)
Status of stocks			
Management classification status	High	Recruitment or growth overfished, overexploited, depleted or "threatened". *Based on IUCN Red List status of "Vulnerable" (IUCN 2006)*	MBA (2004)
Current population abundance relative to B_{MSY}	Unknown	*Unknown*	MBA (2004)
Occurrence of overfishing (current level of fishing mortality relative to overfishing threshold)	High	Overfishing occurring ($F_{curr}/F_{MSY}>1.0$). *Don't have this metric, instead* based *on F/Z ratio of 0.58*	MBA (2004)
Overall degree of uncertainty in status of stock	Int.	Only limited, fisher-dependent data on stock status are available	MBA (2004)
Long-term trend (relative to species'generation time) in population abundance as measured by either fishery-independent (stock assessment) or fishery-dependent (standardized CPUE) measures	High	Trend is down. *Based on multiple population declines from 65-100 % in the Danajon Bank region and inferred declines of 30-50 % from overfishing and habitat degradation (IUCN 2006)*	MBA (2004)
Short-term trend in population abundance as measured by either fishery-independent (stock assessment) or fishery dependent (standardized CPUE) measures	Int.	Trend is flat or variable (among areas, over time or among methods) OR unknown. *Variable using CPUE standardized to fishing nights and otherwise unknown* (K. Martin-Smith, unpublished data)	MBA (2004)
Current age, size or sex distribution of the stock relative to natural condition	Int.	Distributions unknown. *Distributions from fisheries landings are available for 1996-1998 and 2001-2004, and from UVC from Feb-April 2003, but unfished or baseline size/age distributions are otherwise undocumented or anecdotal*	MBA (2004)
Nature and extent of discarded bycatch *(from seahorse fisheries rather than of seahorses in other fisheries)*			MBA (2004)
Quantity of bycatch, including any species of "special concern" (identified as "endangered", "threatened", or "protected" under state, federal or international law)	Low	Quantity of bycatch is low (<10 % of targeted landings on a per number basis) AND does not regularly include species of special concern. *H. comes is targeted and hand-harvested individually by breath-hold divers, so there is no bycatch associated with this fishery*	MBA (2004)

Population consequences of bycatch	Low	Evidence indicates quantity of bycatch has little or no impact on population levels. *No bycatch*	MBA (2004)
Trend in bycatch interaction rates (adjusting for changes in abundance of bycatch species) as a result of management measures (including fishing seasons, protected areas and gear innovations)	n/a	Not applicable because bycatch is low. *No bycatch*	MBA (2004)
Evidence that the ecosystem has been, or likely will be, substantially altered in response to the continued discard of the bycatch species	Low	Studies show no evidence of ecosystem impacts. *Species is not discarded.*	MBA (2004)
Effects of Fishing Pratices on Habitats and Ecosystems			MBA (2004)
Known effects of fishing gear on physical and biogenic habitats	Low	Minimal damage (pelagic longline, midwater gillnet, midwater trawl, purse seine, hook and line, or spear/harpoon). *Hand- gathered by fishers who unwrap seahorses from holdfasts. Minimal damage.*	MBA (2004)
Resilience of physical and biogenic habitats to disturbance by fishing method	n/a	Not applicable because gear damage is minimal. *True*	MBA (2004)
If gear impacts are moderate or great, spatial scale of the impact	n/a	Not applicable because gear damage is minimal. *True*	MBA (2004)
Evidence that the removal of the targeted species or the removal/deployment of baitfish has or will likely substantially disrupt the food web	Int.	Conflicting evidence of ecosystem impacts or unknown. *True*	MBA (2004)
Evidence that the fishing method has caused or is likely to cause substantial ecosystem state changes, including alternate stable states	Int.	Conflicting evidence of ecosystem impact or unknown. *True*	MBA (2004)
Effectiveness of the Management Regime			
Stock status: Management process utilizes an independent scientific stock assessment that seeks knowledge related to the status of the stock	High	No stock assessment available now and none is planned in the near future. *True*	MBA (2004)
Scientific monitoring: Management process involves regular collection and analysis of data with respect to the short and long-term abundance of the stock	High	No regular collection or analysis of data. *True*	MBA (2004)
Scientific advice: Management has a well-known track record of setting catch quotas beyond those recommended by its scientific advisors and other external scientists	n/a	Not enough information available to evaluate OR not applicable because little or not scientific information is collected. *The latter*	MBA (2004)
Bycatch: Management implements an effective bycatch reduction plan	n/a	Not applicable because bycatch is “low”. *True*	MBA (2004)
Fishing practices: Management addresses the effect of the fishing method(s) on habitats and ecosystems	n/a	Not applicable because fishing method is moderate or benign. *True*	MBA (2004)
Enforcement: management and appropriate government bodies enforce fishery regulations	High	Regulations not regularly and consistently enforced. *True*	MBA (2004)
Management track record: conservation measures enacted by management have resulted in the long-term maintenance of stock abundance and ecosystem integrity	Int.	Unknown. *True*	MBA (2004)

APPENDIX I – McGill University Animal Use Protocol - Research



B level

McGill University
Animal Use Protocol – Research
Guidelines for completing the form are available at
www.mcgill.ca/fgsr/rgo/animal/

Protocol #: 3670
Investigator #: 856
Approval End Date: MARCH 31, 2003
Facility Committee: SCI

☐ Pilot ☐ New Application ☒ Renewal of Protocol # 3670

Title (must match the title of the funding source application): Seeking new paradigms in the conservation of exploited seahorse (NSERC) and Community-based seahorse conservation management

1. Investigator Data:

Principal Investigator: Dr. Amanda Vincent
Office #: 398 6455
Department: Biology
Fax#: 398 5069
Address: 1205 ave. Dr. Penfield, Montreal, QC, H3A 1B1
Email: amanda_vincent@maclan.mcgill.c

2. Emergency Contacts: Two people must be designated to handle emergencies.

Name: Dr. Amanda Vincent	Work #: 1 514 398 6455	Emergency #:	514 938 422208
Name: Dr. Melita Samoilys	Work #: 1 514 398 6462	Emergency #:	514 486 0371

3. Funding Source:

External ☒
Source (s): NSERC, John G. Shedd Aquarium, Community Fund (UK), MacArthur/IDRC, Pew Fellowship
Peer Reviewed: ☒ YES ☐ NO**
Status: ☒ Awarded ☐ Pending
Funding period: From: January 1999 To: December 2004

Internal ☐
Source (s):
Peer Reviewed: ☐ YES ☐ NO**
Status: ☐ Awarded ☐ Pending
Funding period:

ACTION	✓	DATE
CCs	✓	July 9'02
DB		
APPROVED		

** All projects that have not been peer reviewed for scientific merit by the funding source require 2 Peer Review Forms to be completed . e.g. Projects funded from industrial sources. Peer Review Forms are available at www.mcgill.ca/fgsr/rgo/animal/

Proposed Start Date of Animal Use (d/m/y): 01/01/99 or ongoing ☐
Expected Date of Completion of Animal Use (d/m/y): 31/12/04 or ongoing ☐

Investigator's Statement: The information in this application is exact and complete. I assure that all care and use of animals in this proposal will be in accordance with the guidelines and policies of the Canadian Council on Animal Care and those of McGill University. I shall request the Animal Care Committee's approval prior to any deviations from this protocol as approved. I understand that this approval is valid for one year and must be approved on an annual basis.

Principal Investigator: x Amanda Vincent Date: 3.5.02

Approval Signatures:

Chair, Facility Animal Care Committee:		Date: JUN 18 2002
University Veterinarian:		Date: July 8, 2002
Chair, Ethics Subcommittee(as per UACC policy):		Date:
Approved Period for Animal Use	Beginning: April 1, 2002	Ending: MARCH 31, 2003

☐ This protocol has been approved with the modifications noted in Section 13.

April 2001

JUL 0 2 [illegible]

APPENDIX II – Waiver From Journal of Fish Biology

Dec. 18, 2007.

Dear Ms. Morgan,

I have received the below query from Dr Craig, Editor of the Journal of Fish Biology.

I confirm that it is possible for you to include your paper within your thesis as long as the terms and conditions below are adhered to.

Best wishes,

Tanya Kneller, Blackwell Publishing.
....
Appendix B: Terms and Conditions
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