

**An information-theoretic assessment of spot-pattern
matching software and its application to population
estimates of whale sharks (*Rhincodon typus*)**

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STATEMENT OF AUTHORSHIP

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institute of tertiary education. Information derived from the published and unpublished work of others has been acknowledged in the text and a list of references given.

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FOREWORD

A section of chapter 2 is published in the journal *Frontiers in Zoology* under the title ‘Spot the match – wildlife photo-identification using information Theory’ (2007) 4:2 doi:10.1186/1742-9994-4-2. Authors of the manuscript are Conrad Speed (CWS), Corey Bradshaw (CJAB) and Mark Meekan (MGM). CWS, CJAB and MGM designed the study, CWS and CJAB did the analysis, and all authors contributed to writing the paper. CWS did most of the analysis with assistance from CJAB, and CWS took the lead in writing the manuscript.

ABSTRACT

I examined the use of an automated spot recognition program that incorporated a novel information-theoretic approach to assess uncertainty for matching of photographs of natural markings of wildlife. This technique was applied to a photo-library of whale sharks (*Rhincodon typus*) from Ningaloo Reef, WA, to make population estimates generated from this library more robust. The information criterion (IC) algorithm I developed resulted in a parsimonious ranking of potential matches of photographs of individuals in an image-matching library. Automated matches were compared to manual-matching (by-eye) results to test the performance of the software and IC algorithm. Limitations of the software relating to the number of spot pairs matched and subject angle were also assessed using the IC algorithm. Validation of matched and non-matched images provided an IC weight threshold (approximately 0.2) below which match certainty was not assured. The majority of images tested were correctly assigned; however, scores for the by-eye comparison were lower than expected, possibly due to the low sample size. I found that the effect of increasing horizontal angle (yaw) of sharks in images reduced matching likelihood considerably, thus highlighting the need for only using images at consistent angles for software matching. There was a negative linear relationship between the number of matching spot pairs and matching score. However, this relationship disappeared, when using the IC algorithm developed, which takes into account the number of matching spot pairs. Population estimates using non-validated and validated image matches were similar to previously obtained estimates of between 300 and 500 at Ningaloo Reef for open population, Jolly-Seber models. The pattern matching software and use of easily applied information-theoretic scores of match parsimony provided a reliable and freely available method for individual identification of wildlife, with wide applications and demonstrated improvements to studies using capture-mark-recapture techniques to describe demographic parameters of populations.

TABLE OF CONTENTS

CHAPTER 1 – GENERAL INTRODUCTION	6
Individual identification techniques for CMR.	8
Assumptions of CMR.	11
Photo-identification.....	12
Computer-aided image matching.....	13
Population models.....	15
<i>Elasmobranch models.</i>	15
Whale sharks.....	17
Pattern matching certainty and information theory.	18
CHAPTER 2 – SPOT THE MATCH – WILDLIFE PHOTO-IDENTIFICATION	
USING INFORMATION THEORY	21
Introduction.....	21
Methods.....	24
<i>Whale shark database & study site.</i>	24
<i>Matching software, fingerprint creation and image matching.</i>	27
<i>I³S matching validation.</i>	32
<i>Assessment of ‘by-eye’ matches using I³S.</i>	34
<i>Effect of horizontal angle on matching success.</i>	34
<i>Assessment of the number of spot pairs compared.</i>	36
<i>Whale shark population size.</i>	37
Results.....	40
<i>I³S matching validation.</i>	40
<i>Assessment of ‘by-eye’ matches using I³S.</i>	43
<i>Testing the effect of horizontal angle on the matching success of I³S.</i>	45
<i>Assessment of Spot #.</i>	45
<i>Whale shark population size using I³S matches.</i>	48
<i>Whale shark population size using validated I³S matches.</i>	50
Discussion.....	53
<i>I³S applications</i>	59
<i>Recommendations</i>	63
<i>Estimating population size</i>	64
Conclusion.....	66
REFERENCES	68
APPENDIX 1. Text output from an I ³ S search.....	76
APPENDIX 2. R code for information criterion algorithm.....	77
APPENDIX 3. Spot the match – wildlife photo-identification using information theory (manuscript).....	78

LIST OF FIGURES

Figure 1 - Example species that could be identified and followed through time using photo-identification.....	10
Figure 2. Study Site – Ningaloo Reef, Western Australia.	24
Figure 3. Image capture of a whale shark at Ningaloo Reef.	25
Figure 4. Measuring total length of a whale shark at Ningaloo Reef.....	25
Figure 5. Structure of the whale shark database.....	26
Figure 6. Fingerprint file creation.....	28
Figure 7. Results of searching an unknown image in I ³ S.....	30
Figure 8. Visual comparison of unknown individual and matched individuals.....	31
Figure 9. Spot cloud of matching spot pairs.....	32
Figure 10. Five angles (0°, 10°, 20°, 30° and 40°) of an individual shark for angle comparison in I ³ S.....	35
Figure 11. Horizontal angle measurement of a shark with Screen Protractor.....	36
Figure 12. I ³ S matching validation IC weights (w_I) for known matched (a) and non-matched pairs (b), and I ³ S matching validation evidence ratios (ER_I) for known matched (c) and non-matched pairs (d).	41
Figure 13. Mean (a) IC weights (w_I) for known matching pairs showing validated and non-validated matches; (b) Mean evidence ratios (ER_I) for known matching pairs showing validated and non-validated matches.	42

Figure 14. (a) Mean IC weights (w_I) for known matching pairs showing validated by-eye matches and non-validated by-eye matches; (b) Mean evidence ratios (ER_I) for known matching pairs showing validated by-eye matches and non-validated by-eye matches.44

Figure 15. (a) Mean IC weights (w_I) for horizontal angle categories, where images at 0° were matched against images skewed by 10, 20, 30 and 40° 46

Figure 16. (a) Relationship between complementary log-log-transformed (clog-log) I^3S scores and \log_{10} -transformed number of spot pairs.47

Figure 17. Mean validated and unvalidated (< 0.2) w_1 for inter-annual resights used for population modelling.....50

Figure 18. Known-matching images that were not matched with I^3S or validated. ...54

Figure 19. A) Spotted eagle ray (*Aetobatus narinari*) showing homogenous spot pattern on dorsal surface, B) Manta ray (*Manta birostris*) ventral surface with sparse, irregular spot pattern.61

Figure 20. Juvenile and adult leopard sharks illustrating the difference in skin patterns between life stages.62

LIST OF TABLES

Table 1. Open-population models for whale shark population re-assessment using MARK.....	38
Table 2. Summary of population size estimates from closed and open populations for I ³ S resights	49
Table 3. Results for model analysis using non-validated (unvalidated) I ³ S dataset	49
Table 4. Summary of population size estimates from closed and open populations for validated I ³ S resights.....	51
Table 5. Results for model analysis using validated I ³ S dataset.....	52

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The successful management and conservation of populations of wildlife require a good understanding of population demographics (Caughley and Gunn 1996) such as distribution, population structure, genetic diversity, reproductive performance, foraging ecology, and survival (Karlsson *et al.* 2005). Populations of wild animals can be thought of as stochastic systems; thus the estimation of demographic parameters can be problematic sometimes given high variability. With the exception of some captive or domestic species, complete data sets of all demographic parameters are typically unavailable to researchers. In this situation, parameters can be modelled using estimates of key variables and with the addition of data on biology, ecology and environmental stochasticity. Model outputs then provide wildlife researchers and managers with a platform on which they can make effective decisions for the conservation or control of wild populations of animals.

The application of mathematical models to a population can assist managers by firstly, permitting hypotheses about the population to be compared with observed data, and secondly, by predicting consequences of potential decisions and associated uncertainty (Thomas *et al.* 2005). For example, modelling of the life history stages of the population structure of the loggerhead turtle (*Caretta caretta*) by Bowen *et al.* (2005) showed that a loss of pelagic juveniles had a diffuse impact on nesting colonies, a loss of sub-adults had a directed impact on nearby breeding colonies and a loss of adults had direct impacts on corresponding breeding populations. These results helped managers decide on the strategy that would be most effective for each life stage in order to maintain or enhance population size.

Often there is a large gap between science and the management of wildlife. Ideally, these should be integrated to provide the most effective results. One such example of how a sound knowledge of population demographics and integrated management is aiding in the conservation of a wild population is the Kenyan Rhino Programme (KRP). By integrating biological management and monitoring strategies, the KRP has provided decision makers with sufficient information to manage the national herd

of eastern black rhinos (*Diceros bicornis*) at the meta-population level (Amin *et al.* 2006). This monitoring program helped the population of eastern black rhinos to increase 5 % in 2005 (Amin *et al.* 2006).

Similarly, strategies for the conservation of wolverine (*Gulo gulo*) populations in Scandinavia have integrated research findings to inform management. Due to culling of the wolverine from the mid 19th century to protect live stock, population numbers dropped, and their survival status was largely unknown. Different management options were modelled using a population viability analysis (PVA), which developed future population projections based on current stock and harvesting strategies (Saether *et al.* 2005). The results indicated that the current quota determined by the management boards was too high to secure viable populations in Norway, and should current practices continue the population would be extinct within a short time period.

In some instances, it may be necessary to model populations of pest species in order to control their numbers. A successful example is the population control of house crows in Singapore (*Corvus splendens*), which was based on appropriate levels of culling determined by population modelling (Brook *et al.* 2003). The Singapore government used this information and was able to successfully reduce the population of crows to the desired level within 2 years. This highlights how the modelling of population demographics can successfully aid in the management of a species via providing managing authorities with reliable data on which to base conservation decisions.

Models are only approximations of reality; biological systems are complex and include many small effects, interactions, individual heterogeneity, and individual environmental covariates that can all complicate estimates (Burnham and Anderson 2002). While stage-based models such as those used by Bowen *et al.* (2005) may be suitable for certain species, it can be difficult to calculate elasticities (such as survival, productivity, growth rate, etc) for these models where few demographic data are available (see. Mollet and Cailliet 2003). Incorrectly calculated elasticities can greatly affect λ (growth or decline of population size over time), and in turn provide managers with misleading model outcomes on which species management is then based.

For population models to provide as accurate approximations of reality as possible, it is essential to collect high-quality data. Even the most advanced models will provide unrealistic estimates of population demographics if unreliable data are used. One of the most prevalent and widely tested methods of estimating key demographic parameters such as survival, movement rate, capture probability and age structure is capture-mark-recapture (CMR). In CMR studies, animals are initially identified and then released back into the population for subsequent sampling (Schwarz and Seber 1999). During the subsequent sampling events, animals that have and have not been previously identified are sampled, and so on over multiple sampling events. From this information, population demography such as population size can be estimated via simple equations such as the Lincoln-Peterson estimator (Seber 1982).

Individual identification techniques for CMR. A Key requirement of CMR is that animals can be individually recognised so that they can be followed through time, thus allowing demographic rates like survival to be estimated (Lebreton *et al.* 1992). Individual recognition can be achieved by applying an artificial mark to an animal or by using an animal's natural markings (Neumann *et al.* 2002). The former technique is pervasive in ecological studies, ranging from the purely theoretical (e.g., Booth 2004) to the highly applied (e.g. Kohler and Turner 2001), and has been used in both the marine and terrestrial realms on taxa ranging from insects (e.g., Auckland *et al.* 2004) through to whales (e.g., Watkins *et al.* 1993). However, applying artificial marks to wildlife, can alter natural behaviour and reduce individual performance (e.g., Gauthier-Clerc *et al.* 2004). The marking process itself may be disruptive (Bateson 1977) due to the necessity of handling and restraining for mark application (Ogutu *et al.* 2006), and the loss of marks over time (Bradshaw *et al.* 2000), and the non-reporting of retrieved marks (Schwarz and Seber 1999) may potentially cause a severe bias in parameter estimates (Stevick *et al.* 2001). Additionally, there are often a host of ethical and welfare issues that can arise from the application of permanent or semi-permanent marks (McMahon *et al.* 2006, Wilson and McMahon 2006). The artificial marking of individuals may also be costly and impractical when dealing with large populations (Kelly 2001).

To address some of these problems, the identification of individual animals from their natural markings has become a major tool for the study of some animal populations

(Stevick *et al.* 2001), and has been applied to an equally wide range of animals from badgers (Dixon 2003) to whales (Sears *et al.* 1990, Fujiwara and Caswell 2001). The use of natural patterns to identify individuals in a population can potentially be extended to include not only vertebrate species, but also invertebrates (Fig.1).

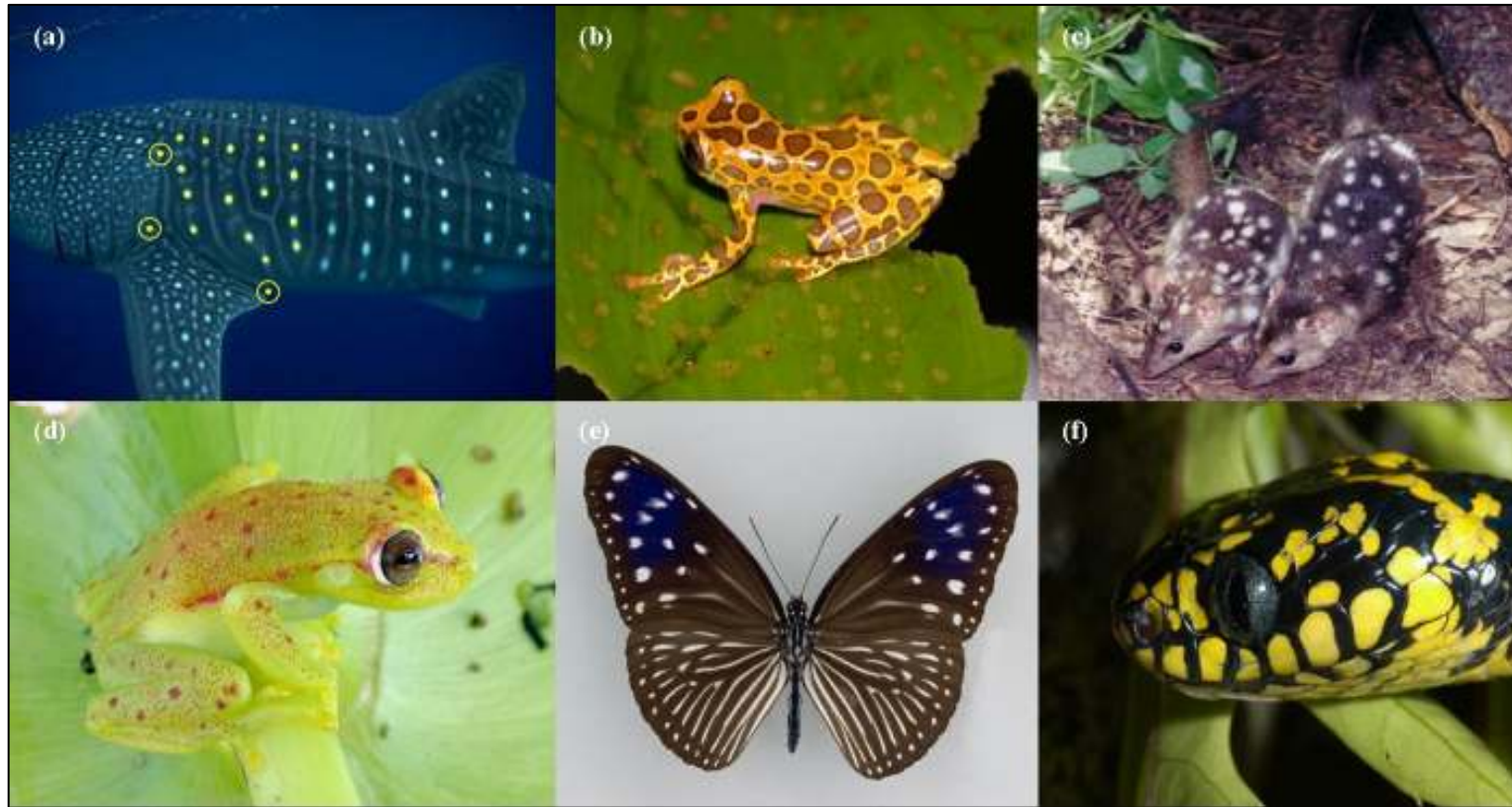


Figure 1 - Example species that could potentially be identified and followed through time using photo-identification. Shown are (a) whale shark (*Rhincodon typus*) showing the reference area defined as the area encompassed by the reference points (yellow circles); (b) spotted tree frog (*Hyla leucophyllata*); (c) northern quoll, (*Dasyurus hallucatus*); (d) Amazon spotted frog (*Hyla punctata*); (e) striped blue crow (*Euploea mulciber*); and (f) mangrove snake (*Boiga dendrophilia*).

Non-invasive methods rely on natural markings or other characteristics such as notches, scars, patches and blotches on an animal's body (Gope *et al.* 2005). These methods are generally less expensive when compared to traditional methods of tagging (Karlsson *et al.* 2005), fewer personnel are needed to make resights, and other research objectives can be achieved while resighting (Minta and Mangel 1989). Not only are these methods useful when dealing with animals such as whales where legal obstacles prevent the use of conventional tagging methods (Kehtarnavaz *et al.* 2003 & Gope *et al.* 2005), but also when dealing with potentially dangerous animals such as lions (e.g. Ogutu *et al.* 2006), tigers (e.g. Karanth and Nichols 1998) and some species of shark (e.g. Anderson and Goldman 1996). Scarring and other semi-permanent markings may be transient or multiply between sightings, which can make it difficult to re-identify individuals accurately (Castro and Rosa 2005 & Dixon 2003). Therefore, it is ideal to use permanent and unique differences in pigmentation in skin or pelage of animals for identification purposes because they appear to be the most reliable (Pennycuik 1978 & Domeier and Nasby-Lucas 2006).

Assumptions of CMR. When employing CMR methods for demographic estimation there are a number of important assumptions that require careful examination (Schwarz and Seber 1999) to ensure that the most accurate model outputs are achieved. These assumptions are applicable to both traditional tagging methods as well as methods that use natural marks; however, potential problems can manifest themselves in differing forms and have differing effects on estimates.

Assumptions common in CMR studies are outlined by Seber (1982) and include: (1) the probabilities of recapture and survival between resights are homogeneous, (2) all tags are retained and reported, (3) marked individuals randomly disperse within the population and (4) non-marked individuals have an equal probability of capture (equal catchability). This latter assumption is a major consideration of CMR models, yet it persists as being one of the greatest sources of confounding variation (Minta and Mangel 1989). CMR based on photo-identification allows many of the violations of equal catchability to be accommodated for (Minta and Mangel 1989). This is mainly due to the fact that the alteration of natural behaviour by physical restraint during tagging is not an issue.

The ability to mark and subsequently identify the same individual repeatedly is also a principle assumption of CMR studies, which is violated if tag loss or non-reporting of a tag occurs. These errors of identification can potentially inflate population estimates (Stevick *et al.* 2001) and can be largely avoided if using a natural marking system (Minta and Mangel 1989), provided there is little ambiguity when matching, (which is almost never the case). Such studies do not have to be concerned with tag loss as such, but the changing of scarring between sampling periods is considered equivalent to tag loss (Stevick *et al.* 2001). It is however, possible to incorporate tag loss estimates into demographic estimates of a population (Bradshaw *et al.* 2003), or incorporate tag loss directly into CMR models (Cowen and Schwarz 2006). The failure to re-identify an individual is not unlike non-reporting of an artificial tag (Stevick *et al.* 2001), and can affect demographic estimates in a similar fashion. Due to the non-invasiveness of this technique, it is also more likely that individuals will disperse within the population in a non biased fashion. A violation of any of the aforementioned assumptions can lead to a bias in point estimates of survival and capture probability (Williams *et al.* 2001) and should be avoided or incorporated as uncertainty into models.

Photo-identification. Photo-identification is one of the more effective and popular methods of recording natural markings of an animal because it permits individual identification, which can then allow the study of animal movement patterns, site fidelity, population size and other population parameters (Karlsson *et al.* 2005), with the only field requirement being a suitable camera. In addition to the other benefits of non-intrusive ‘marking’ of individuals, this method also allows storage of photos in a library for cross-matching and generation of capture-history matrices (Fujiwara and Caswell 2001, Meekan *et al.* 2006; Bradshaw *et al.* 2007). There have been an increasing number of photo-identification studies of long-lived animals that rely on natural markings (Kelly 2001). These studies include predatory cats (Kelly 2001, Ogutu *et al.* 2006, Maffei *et al.* 2004 & Karanth and Nichols 1998), cetaceans (Hammond *et al.* 1990), and elasmobranchs (Arzoumanian *et al.* 2005, Meekan *et al.* 2006 & Domeier and Nasby-Lucas 2006, Van Tienhoven *et al.* in revision).

Image capture techniques vary between studies based largely on accessibility to study animals. In recent photo-identification studies, images have mainly been captured

using digital cameras or video cameras. Images may be captured directly on land (Kelly 2001), remotely by camera trap (Maffei *et al.* 2004 and Karanth and Nichols 1998), by aerial photography (Hiby and Lovell 2001), on the surface of the ocean (Langtimm *et al.* 2004 and Parra *et al.* 2006,) as well as underwater (Corcoran and Gruber 1999, Arzoumanian *et al.* 2005, Castro and Rosa 2005, Meekan *et al.* 2006, Domeier and Nasby-Lucas 2006 and Van Tienhoven *et al.* 2007). Underwater photography has an additional host of problems that are not associated with standard photographic techniques (Meekan *et al.* 2006), such as light refraction and backscatter from particulate matter in the water. These issues, as well as the complicating factor of maintaining the line of sight of animals being photographed, can make underwater photo-identification particularly challenging. Although photo-identification is gaining favour as a reliable method of CMR, it is not without its limitations; one of the most pertinent being problems associated with the manual identification and matching of individuals by eye.

Computer-aided image matching. In photo-identification studies, photograph libraries can be examined manually (by eye) to build a history of individual matches (Meekan *et al.* 2006); however, as the number of photos in a library increases beyond a person's capacity to process the potential candidate matches reliably, the development of faster, automated techniques to compare new photographs to those previously obtained is required (Mizroch *et al.* 1990, Arzoumanian *et al.* 2005). Several automated matching algorithms have been trialled with some success (e.g., Mizroch *et al.* 1990, Wilkin *et al.* 1998, Evans 2003, Hillman *et al.* 2003, Arzoumanian *et al.* 2005, Lapolla 2005, Urian 2005), but these are often highly technical, species/morphological feature specific, or unavailable for public use.

Computer-aided matching software for photo-identification purposes started to emerge during the 1990s, and mainly focussed on identification of marine mammals. Initially these systems were used purely as a means to reduce the number of possible matches to search within manually. An example is a categorical fluke pattern matching program for humpback whales (*Megaptera novaeangliae*), which involved labelling pictures based on 1 of 38 predetermined fluke patterns. An affine movement invariant algorithm was later developed to match fluke patches of humpback whales (*Megaptera novaeangliae*) and gray whales (*Eschrichtius robustus*). This system

includes algorithms for patch extraction, transformation of patches and matching. Although this system is far more advanced than the initial system used for humpback photo-identification, it still requires the user to make the final decision over potential matches.

A computerised version of dorsal fin ratio (DR) extraction for dolphin identification was developed, however this method had limited success at identifying individuals in large databases due to the algorithm's inability to accurately represent the shape of fins (Kreho *et al.* 1999). A further refinement of the dolphin identification system was developed based on a string matching system, which incorporates edge detection and curvature (Araabi *et al.* 2000). This system has wider applications than dolphin identification, and can potentially be used for other organisms with distinct notches in their fins. An affine invariant curve matching system was later developed to match fin edges of marine mammals and was applied to sea lion, gray whale and dolphin photo-identification databases (Gope *et al.* 2005). This system was proven to be superior to the previous string matching system as it further reduces manual labour time.

A three-dimensional system of matching pelage patches of grey seals (*Halichoerus grypus*) was developed at the beginning of the 1990s (Hiby and Lovell 1990) and later adapted for aerial photography (Hiby and Lovell 2001). This system was developed to cope with issues common to previously used two-dimensional matching algorithms such as non-planar surfaces of animals and changes of natural patterns with camera angles (Kelly 2001). Using a three-dimensional model for an animal is obviously more realistic than a two-dimensional model; however, creation and use of three-dimensional models are extremely complex, expensive and time consuming.

Kelly (2001) divided the previously discussed computer-aided matching systems into two major categories: 1) computerised hand-sorting and 2) computerised three-dimensional models. Computerised hand-sorting uses unique identifying features of an individual that are given codes, which then allow for comparison with other individuals in the database (e.g Mizroch *et al.* 1990). The other variations of this method is the tracing of an outline of a feature of an animal, which can then be compared with other individuals in the database (e.g., Whitehead 1990, Kehtarnavaz

et al. 2003 and Gope *et al.* 2005). The second type of computer-aided matching system are computerised three-dimensional models, which align images with a three-dimensional model of a body part, which allows comparison of features regardless of the orientation to the camera (Kelly 2001).

Both methods outlined have differing advantages and disadvantages; however, one issue that affects both is the quality of photos included in photographic databases. If photos of poor quality are included, or animals in photos lack distinctiveness (Friday *et al.* 2000) then either methods will yield unreliable matches, which can affect demographic estimates.

Population models. Understanding the extinction process and determining factors for species persistence are the underlying themes of conservation biology (Shaffer 1990). Studying life history parameters assists in the understanding of population dynamics and ecological issues (Lebreton *et al.* 1992) that may threaten a population. These parameters may include population size, stage structure, average per-capita birth and death rates, as well as demographic and environmental stochasticity. As previously outlined, it is possible to estimate and model population demographics and environmental effects of a population based on CMR data collected in the field. The reliability of these estimations will be reflected by the quality of the data collected and model selection. Model selection using CMR techniques is largely based on whether data adhere to the assumptions (Seber 1982) discussed previously, and the availability of biological information that will influence the structure of models (Miller *et al.* 2003).

Elasmobranch models. Numerous examples of elasmobranch modelling from CMR studies exist within the literature (e.g. Frisk *et al.* 2002, Mollet and Cailliet 2002, Meekan *et al.* 2006 and Bradshaw *et al.* 2007); however providing accurate estimations of demography for elasmobranchs is exceedingly challenging. This is due to a number of reasons; 1) there is often little information on vital parameters such as survival rates available (Mollet and Cailliet 2003), 2) many species may have complex reproductive physiologies that include resting stages, long gestation periods, ovipary or ovovivapory (Mollet and Cailliet 2002), 3) validated age for elasmobranchs are rare in comparison to species of teleosts (Miller *et al.* 2003), and 4)

the decoupling of age and size in many species (Mollet and Cailliet 2002). Furthermore, the distorted elasticity patterns derived from stage-classified models (Mollet and Cailliet 2003) have confounded these issues (Bradshaw *et al.* 2007).

There are numerous demographic studies of elasmobranchs that derive data from traditional tagging approaches (See review by Kohler and Turner 2001), whereas demographic studies of elasmobranch populations based on identifying individuals by their natural variation in pigmentation are relatively uncommon (Castro and Rosa 2005). Indeed this form of CMR has only recently been extended to species such as spotted eagle rays *Aetobatus narinari* (Corcoran and Gruber 1999), white sharks *Carcharodon carcharias* (Domeier and Nasby-Lucas 2006) and whale sharks *Rhincodon typus* (Arzoumanian *et al.* 2005 & Meekan *et al.* 2006; Bradshaw *et al.* 2007).

A study on nurse sharks (*Ginglymostoma cirratum*) by Castro and Rosa (2005) demonstrated for the first time that it is possible to estimate the population sizes of a species of shark based on a photo-identification of natural markings. Two estimators were used in this study, a modified version of the Peterson estimator and the Jolly-Seber (JS) estimator. Due to the reliance on wounding and scarring for individual identification, they were unable to include individuals without distinct markings, which is an issue for many photo-identification studies (Karlsson *et al.* 2005). The reason that this is a problem for CMR is that it violates the assumption of equal catchability assumed by the JS model. An additional issue in that study was the potential for false negatives, where individuals incurred new scars and wounds between sightings. This also violates assumptions of no tag loss, or non-reporting of a tag. Thus, using skin pigmentation patterns instead of scarring is ideal for CMR and estimating population demographics, as long as all individuals have unique, stable marking over time.

A study of the whale shark population by Meekan *et al.* (2006) demonstrated that it was possible to estimate the population size of sharks based on such natural variation of skin pigmentation. Furthermore, the same dataset was used to estimate survival and potential population trajectories (Bradshaw *et al.* 2007). Both of these studies relied on photo-identification data where images were matched manually.

Consequently, like all photo-identification studies to date, the strength of image matches and individual resights were not validated statistically.

Whale sharks. Whale sharks (*Rhincodon typus*) are the largest fish in the world and only one of three species of filter-feeding sharks (Last and Stevens 1994). Whale sharks are listed as being *Vulnerable* by the World Conservation Union (www.redlist.org; Cavanagh *et al.* 2003), and they are listed on Appendix II of the Convention of Migratory Species (CMS) and Annex I (Highly Migratory Species) of the UN Convention on the Law of the Sea (UNCLOS) (CMS 2005). Like other species of elasmobranchs, whale sharks have an apparent *K*-selected life history (Cavanagh *et al.* 2003), which implies they invest their reproductive efforts in producing relatively few, large and well developed offspring, have extended longevity, and are slow to reach sexual maturity (MacArthur and Wilson 1967). These life history traits can often signify low productivity and poor recovery potential (Smith *et al.* 1998, & Walker 1998). Furthermore, the sensitivity of population growth rates to minor variations in survival leaves this species vulnerable to disturbances such as fishing pressure (Bradshaw *et al.* 2007).

Another trait that confounds the issue of a *K*-selected life history is the highly migratory nature of whale sharks (Cavanagh *et al.* 2003). Whale sharks migrate thousands of kilometres (Eckert *et al.* 2002), which means there is the potential for this species to travel between areas where they are protected from harvesting and areas where they are targeted by fisheries (Meekan *et al.* 2006). Whale sharks leaving an aggregation that occurs at Ningaloo Reef, WA have been found to travel into South-East Asian waters (Wilson *et al.* 2005), where fishing is likely to occur. While the harvesting of whale sharks is now prohibited in a number of countries (e.g. Belize, Honduras, Maldives, Philippines, Thailand, India, USA and Australia) (Chen and Phipps 2002), it is probable that past fisheries have contributed to the current fragile status of this species. Whale sharks are still targeted for their fins and flesh in many regions, especially in Southeast Asia (Joung *et al.* 1996) where the demand for their products is high. It is increasingly difficult to monitor and control activities which threaten whale sharks in developing countries where resources are limited. Therefore, several past and present satellite tagging studies (Eckert and Stewart 2001, Eckert *et*

al. 2002, Norman 2004, & Wilson *et al.* 2005) have been trying to determine whale shark movement patterns, thereby assisting global conservation initiatives.

This species has been the subject of several photo-identification studies (Arzoumanian *et al.* 2005, Meekan *et al.* 2006), some of which have already provided valuable information on population size and structure, survival and population trends (Meekan *et al.* 2006; Bradshaw *et al.* 2007) under the supported assertion that the spot and stripe marking patterns of animals are individually unique and temporally stable (Booth 2004; Meekan *et al.* 2006). The initial assessment of the structure of one population's structure at Ningaloo Reef, (Meekan *et al.* 2006) has been complicated by the addition of many hundreds of photographs taken during analogous research programs elsewhere in Australia, Belize, USA, Philippines, Mexico (CITES 2000), as well as Djibouti, Seychelles and Mozambique. Consequently, the number of photographs available has exceeded the number that can be reliably matched by eye, thereby necessitating an automated system of matching. One such system has been developed from an algorithm originally designed for stellar pattern recognition, and is currently being employed by the ECOCEAN whale shark database (Arzoumanian *et al.* 2005). This system has great potential; however, the procedure for entering and matching patterns is complex, and neither the algorithm nor results are publicly available.

Pattern matching certainty and information theory. Available software for matching the natural variation of patterns on animals, (previously discussed), incorporate differing algorithms of varying complexities. A series of packages were developed based on algorithms which use DR, curvature, curve matching and string matching to identify individual marine mammals (Araabi *et al.* 2000, Kehtarnavaz *et al.* 2003, and Gope *et al.* 2005). The algorithms are variations of one another used to achieve the same goal, which is to reduce the number of potential matches to be made by eye. A three-dimensional algorithm developed by Hiby and Lovell (1990), which was employed to match pelage of gray seals (Karlsson *et al.* 2005) and cheetahs (Kelly 2001), provides a match correlation based on positioning error and similarity scores between images. Despite the sophistication and complexity of the algorithms incorporated, the final matching must also be made by eye. A recent addition to the suite of pattern-matching packages was the algorithm adapted from a stellar pattern

recognition algorithm, used for identification of whale sharks (Arzoumanian *et al.* 2005). This algorithm is insensitive to image magnification, rotation, and inversion via the use of triangulated triplets of coordinates, which can then be used to match similar patterns from the database (Arzoumanian *et al.* 2005). This method is almost completely automated, but like the other methods described above, the final validation process involves a manual by-eye component. Furthermore, the uncertainty in the matching algorithms incorporated into all of the software packages outlined have never been reliably contextualised within a multi-model inferential framework (Burnham and Anderson 2002), and so subjective manual matching is still required to determine accuracy and reliability.

One method of obtaining match certainty, which would provide the strength of matches relative to other images considered, is via the use of information theory (see Guiasu 1977 and Burnham and Anderson 2002). An information-theoretic approach for assessing the strength of matches would provide the user with a relatively non-subjective measure, which has so far been unexplored for matching natural markings of wildlife. Therefore, a simple and reliable algorithm that is accessible to the public and is able to incorporate match certainty, is needed for photo-identification studies involving large image libraries.

The principle aims of this study are two-fold (1) to assess the reliability of a simple, freely available software package that recognises spot patterns for use in photo-identification studies of wildlife, and (2) to apply this technique to validate estimates of the whale shark population size at Ningaloo Reef, Western Australia.

The specific aims are to:

- 1) Validate computer-assisted image matches using a novel information criterion (IC) algorithm to provide a measure of match parsimony relative to all matches considered;
- 2) Compare known matches made by eye with the matching software and IC algorithm;
- 3) Assess the effect of variation in horizontal angle of subjects in matching reliability, as well as how the number of spots pairs in matched images affects matching performance;
- 4) Re-analyse population size estimates for whale sharks using the matching software and the information criterion algorithm.

Although I focus on whale sharks as an example system, the application of the computer package and the information-theoretic matching algorithms developed can be applied to any marine or terrestrial species demonstrating some form of stable spot patterning. I demonstrate how a reliable, non-intrusive method of CMR can be used to make robust estimates of population demographics.

Introduction

Effective approaches for the management and conservation of wildlife populations require a sound knowledge of population demographics (Caughley and Gunn 1996). Such information is provided by studies that recognise individual animals so that their fate can be followed through time, thus allowing for the estimation of demographic rates (Lebreton et al. 1992). Individuals can be recognised either by applying an artificial mark to an animal or by using an animal's natural markings (Neumann et al. 2002). The former technique is pervasive in ecological studies from the purely theoretical (e.g., Booth 2004) to the highly applied (Kohler and Turner 2001), and has been used on both marine and terrestrial species from insects (e.g., Auckland et al. 2004) to whales (e.g., Watkins et al. 1993). Unfortunately, applying artificial marks can alter natural behavior and reduce individual performance (e.g., Gauthier-Clerc et al. 2004). The marking process itself may also be disruptive (Bateson 1977) due to handling and restraining for mark application (Ogutu et al. 2006). The loss of marks over time (Bradshaw et al. 2000) and the non-reporting of retrieved marks (Schwarz and Seber 1999) can also compromise demographic estimates. Additionally, ethical and welfare issues can arise from the application of permanent or semi-permanent marks (McMahon et al. 2006, Wilson and McMahon 2006).

To avoid these issues, the identification of individual animals from their natural markings has become a major tool for the study of some animal populations (Stevick et al. 2001), and has been applied to an equally wide range of animals from badgers (Dixon 2003) to whales (Sears et al. 1990, Fujiwara and Caswell 2001). Photo-identification is a popular technique of recording these markings, which allows storage of photos in a library for cross-matching and generation of capture matrices (Fujiwara and Caswell 2001, Meekan et al. 2006). These libraries can be examined manually to develop individual resights (Meekan et al. 2006); however, as the number of photos in a library increases beyond a person's capacity to process the matches manually, the development of automated techniques is required (Mizroch et al. 1990, Arzoumanian et al. 2005). Several automated matching algorithms have been trialed

with some success (e.g., Wilkin *et al.* 1998, Evans 2003, Hillman *et al.* 2003, Arzoumanian *et al.* 2005, Lapolla 2005, Urian 2005), but these are generally highly technical and specialised. Furthermore, uncertainty in the matching algorithms themselves have never been contextualised within a multi-model inferential framework (Burnham and Anderson 2002), and so subjective manual matching is still required to assess reliability (Kelly 2001).

An example taxon that lends itself well to the development and application of a generalist algorithm for photo matching is the world's largest fish – the whale shark (*Rhincodon typus*). This species has been the recent subject of several photo-identification studies (e.g. Arzoumanian *et al.* 2005, Meekan *et al.* 2006), some of which have already provided valuable information on population size (Meekan *et al.* 2006) and survival (Bradshaw *et al.* 2007) under the supported assertion that the spot and stripe patterns of animals are individually unique and temporally stable (Meekan *et al.* 2006). The initial assessment of the demography of one population (Ningaloo Reef, Western Australia – Meekan *et al.* 2006) has been complicated by the addition of many hundreds of photographs taken during analogous research programs in other regions. Consequently, the number of photographs available has exceeded the number that can be reliably matched by eye, thereby necessitating an automated system of matching. One such system has been developed from an algorithm originally designed for stellar pattern recognition, and is currently being employed by the ECOCEAN whale shark database (Arzoumanian *et al.* 2005). This system has great potential; however, the procedure for entering and matching patterns is complex, and neither the algorithm nor results are publicly available. Therefore, a simple, yet reliable algorithm accessible to the public is needed to incorporate a large number of photographs from a wide range of researchers, tourist operators and private organisations.

The aim of this paper is to assess the reliability of a simple, freely available software package that recognises spot patterns for use in photo-identification studies of wildlife. I apply this technique to population estimates of whale sharks (*Rhincodon typus*), as a means of validating the strength of image matches. Although I focus on whale sharks as an example system, the application of the computer package and the information-theoretic matching algorithms developed can be applied to any marine or

terrestrial species demonstrating some form of stable spot patterning (e.g., sharks, cheetahs, lizards, butterflies, etc. – Fig.1). I assess the reliability of this package by comparing known matches made by eye. I also determine the effect of variation in the horizontal angle of subjects in matching reliability, as well as how the number of spots pairs in matched images affects matching performance. All matching results are developed within a fully information-theoretic framework that incorporates all of the uncertainty associated with the matching algorithm, thus aiding users in providing reliability assessments to their matches, and the resulting capture histories and demographic estimates. As such, I provide a novel and parsimonious method for assessing the reliability of pattern matching for capture-mark-recapture purposes, applicable to a wide range of naturally identifiable wildlife species.

Methods

Whale shark database & study site. At present, the photo-library contains 797 photos taken by researchers and tour operators during the months of March to July from 1992-2006 at Ningaloo Reef (21° 47' S, 32° 34' S), Western Australia (Fig.2). The method of image capture between 1992 and 2006 varied over time so that still photographs; video and digital images were all incorporated into the library.

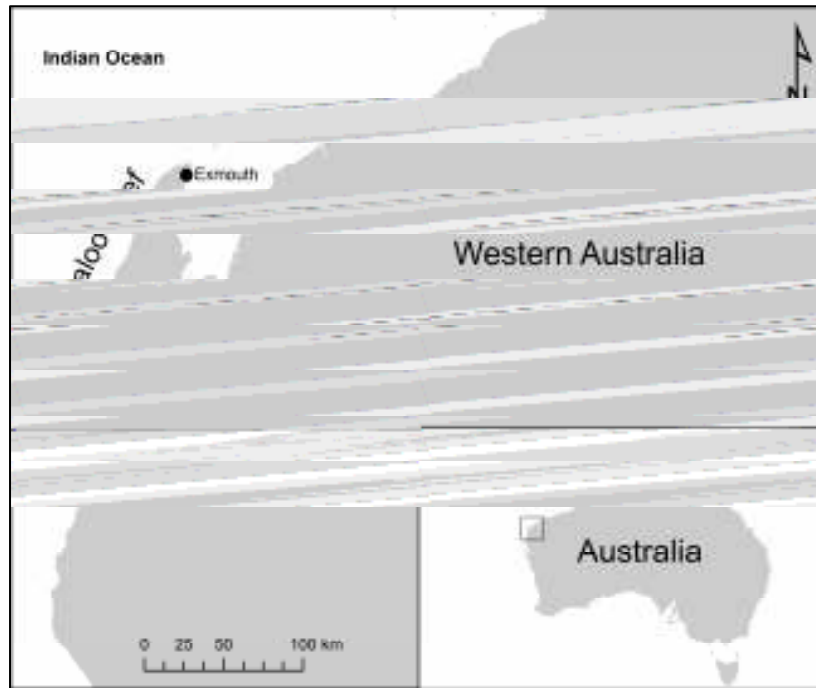


Figure 2. Study Site – Ningaloo Reef, Western Australia.

I assisted in data collection for the 2006 whale shark season, where video footage was captured by C. McLean (Fig.3). Video footage was captured as part of a larger study which aimed to collect genetic samples as well as deploy satellite tags to track the movement of individual whale sharks (Wilson *et al.* 2005). A spotter plane was initially used to locate sharks and a research vessel acted as a mobile work station from which animals could be pursued. My specific tasks during the field trip were to measure the total length of individuals and their dorsal fin height (Fig.4), as well as determine their sex. Additionally, I assisted in trialing new biopsy techniques. Sex and size data were included in the meta-database for subsequent estimation of demographic parameters.



Figure 3. Image capture of a whale shark after attachment of a satellite tag (on dorsal fin) at Ningaloo Reef. This image shows how both video footage, and underwater stills were captured.



Figure 4. Measuring total length of a whale shark at Ningaloo Reef, showing measuring tape held between 2 people.

The main whale shark photo-identification database consists of a photo-library of all photographs collected to date, as well as a photo-library consisting of only images that can be used for computer matching. This photo-matching library is split into left side (LS) and right side (RS) photo-libraries because the matching software only permits matching one side at a time. A Microsoft Access© meta-database containing image specifics and biological information of individuals is linked to the photo-libraries. This system not only permits linkage of the photo-libraries with the metadata, it also provides connectivity of raw metadata with analysed data. The analysed datasheets in the meta-database include a capture matrix, as well as population size, structure and survival estimates (Fig.5).

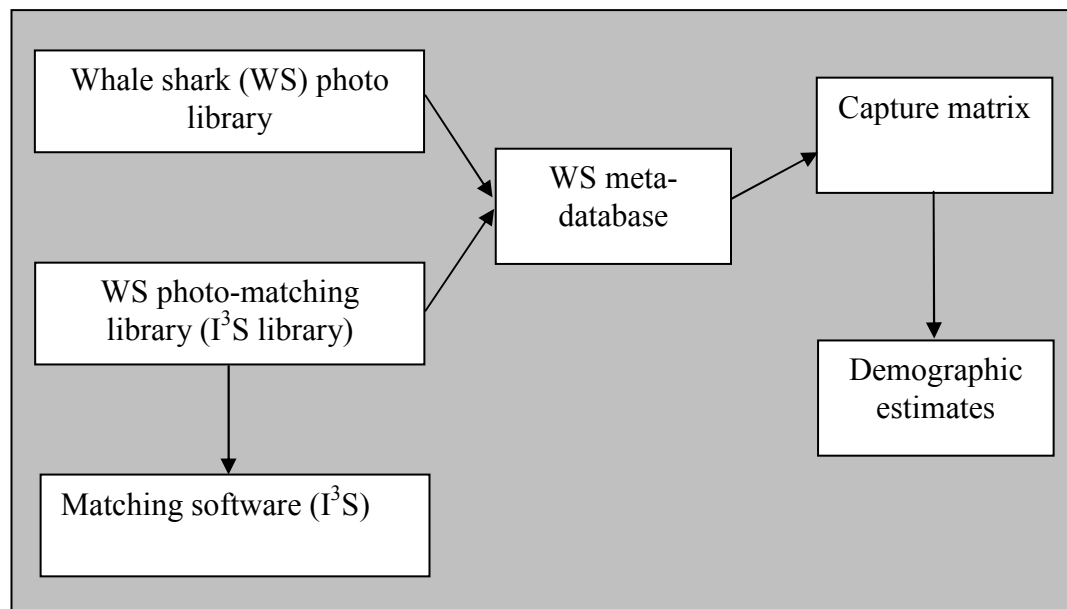


Figure 5. Structure of the whale shark database showing connectivity of matching software, images and metadata.

Prior to this study, all images included in the database had differing nomenclature that followed naming rules specific to each photographer. It was therefore imperative to rename all images in the database using an informative, standardised nomenclature so that a logical organisation of the existing and future photos could be made. It was also important that the name of each image was individually unique to avoid database and image-matching problems. The standardised nomenclature that was chosen included an abbreviation of the location where the photo was taken, the date the photo was taken, the sex of the animal, the side of the animal the photo represented (left or right side), the type of photo (i.e., digital, video, or print), the number of the photo

taken at that sighting, and a letter that indicates the order in which that shark was seen on that day. An example name follows:

NIN.05041992.M.L.VID.GT.3b

This example describes an image taken at Ningaloo Reef (NIN), on the 5th of April 1992. The shark was a male (M) and the photo was of the left side of the shark (L). The image was captured using video (VID) and the video was taken by Geoff Taylor (GT). The '3' indicates that this is the 3rd image in a series of images captured of this shark at that sighting, and the 'b' indicates that it was the second shark seen on that day. There are a few images in the new database that still have their original naming due to the fact that metadata was unavailable at the time of renaming. These metadata may be obtainable from the photographer at a later date.

Matching software, fingerprint creation and image matching. The software known as Interactive Individual Identification System (I³S), originally designed to match natural variation in spot patterns of grey nurse sharks (*Carcharias taurus*), was used to create 'fingerprint' files and match individuals. Fingerprint files are used to identify individual whale sharks based on their spot pattern, in a fashion analogous to the concept of human fingerprint recognition. The area on the flank of sharks directly behind the 5th gill slit was selected as the most appropriate area to use for identification of whale sharks. This area was chosen based on consistency with past studies, and due to the ease that photographers can focus on this area (Arzoumanian *et al.* 2005 and Meekan *et al.* 2006). The positioning of spots in this area was also less likely to be distorted due to undulation of the caudal fin, which may affect the matching success of I³S.

The initial procedure once an image was entered into the database was to create a fingerprint file. Three reference points were required by I³S, and I chose points that could be easily and unambiguously identified in each photo: 1) the top of the 5th gill slit, 2) the point on the flank corresponding to the posterior point of the pectoral fin and 3) the bottom of the 5th gill slit (Fig.6).



Figure 6. Fingerprint file creation (reference points and spot highlighting shown).

After the initial reference points for each image were entered, the centres of the most obvious spots within and slightly posterior to the reference area were highlighted by the operator. The reference area includes the spots behind the 5th gill slit, below the uppermost longitudinal ridge, and in front of the start of the dorsal fin. I³S requires a minimum of 12 spots to be highlighted to form a fingerprint, and a maximum of 40 spots. Highlighting spots outside of the immediate reference area can affect the ability of the I³S matching algorithm (Hartog, J, pers. com.); therefore, highlighted spots were kept roughly within the reference area for fingerprinting. I created all of the fingerprints currently available in the whale shark database, and highlighted between 25 and 35 spots per fingerprint.

The requirement of all three reference points to be visible in the photograph for a fingerprint to be created meant that not all 797 photos could be used. As such, I could

use 433 (54 %) of the original photographs, of which 212 were of the LS and 221 were of the RS of the shark. To compare fingerprints of sharks, a common reference system is required, which is achieved by using a two-dimensional affine transformation (Van Tienhoven *et al.* 2007). The transformation is calculated as follows:

$$M \begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} m_{11} & m_{21} \\ m_{12} & m_{22} \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} + \begin{pmatrix} t_1 \\ t_2 \end{pmatrix} = \begin{pmatrix} m_{11}x + m_{21}y + t_1 \\ m_{12}x + m_{22}y + t_2 \end{pmatrix} \quad \text{Equation 1}$$

where M is the affine transformation matrix of x and y , and m_{11} , m_{21} , m_{12} , m_{22} , t_1 and t_2 are unknown variables (Van Tienhoven *et al.* 2007).

Two search functions are available in I³S, a ‘quick search’ and an ‘exhaustive search’. The quick search only uses the 3 reference points as a first approximation, however; the exhaustive search uses a large number of affine transformations to get the best possible match (Van Tienhoven *et al.* 2007). The search function in I³S compares the new fingerprint file against all of the other fingerprint files in the database by using a two-dimensional linear algorithm. The algorithm calculates the sum of the distances between spot pairs divided by the square of the number of spot pairs (Hartog and Reijns 2004). The matching algorithm is calculated as follows:

$$\frac{\sum d}{n^2} \quad \text{Equation 2}$$

Where d is the distance between matching spot pairs and n is the number of matching spot pairs. The matched spot pairs with the minimum overall sum of the squared distances between them is the most likely match, and given a score from 1 to 0 (0 being a perfect match). The program also lists the next 49 most likely spot pair matches, which it ranks in decreasing order of likelihood (Fig.7). The next step is to look at the most likely match, which is ranked as the top of the list of 50 matches. I³S provides a visual match of the unknown image and the image with which it was matched (Fig.8). A visual display of the matching spot pairs called a ‘spot cloud’ is also available to assist in matching individuals (Fig.9).

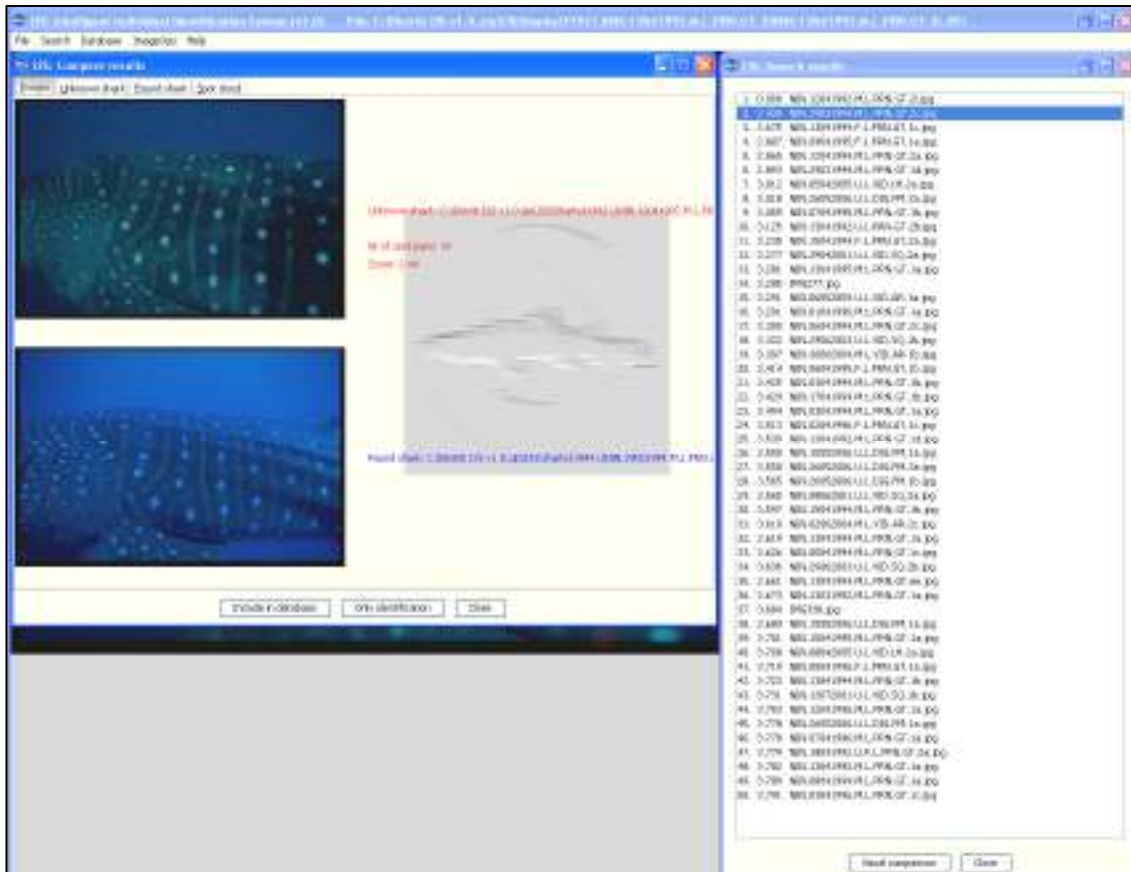


Figure 8. Visual comparison of unknown individual and matched individuals (left side of the screen). The top image is unknown, and the bottom image is the matched image from the database.

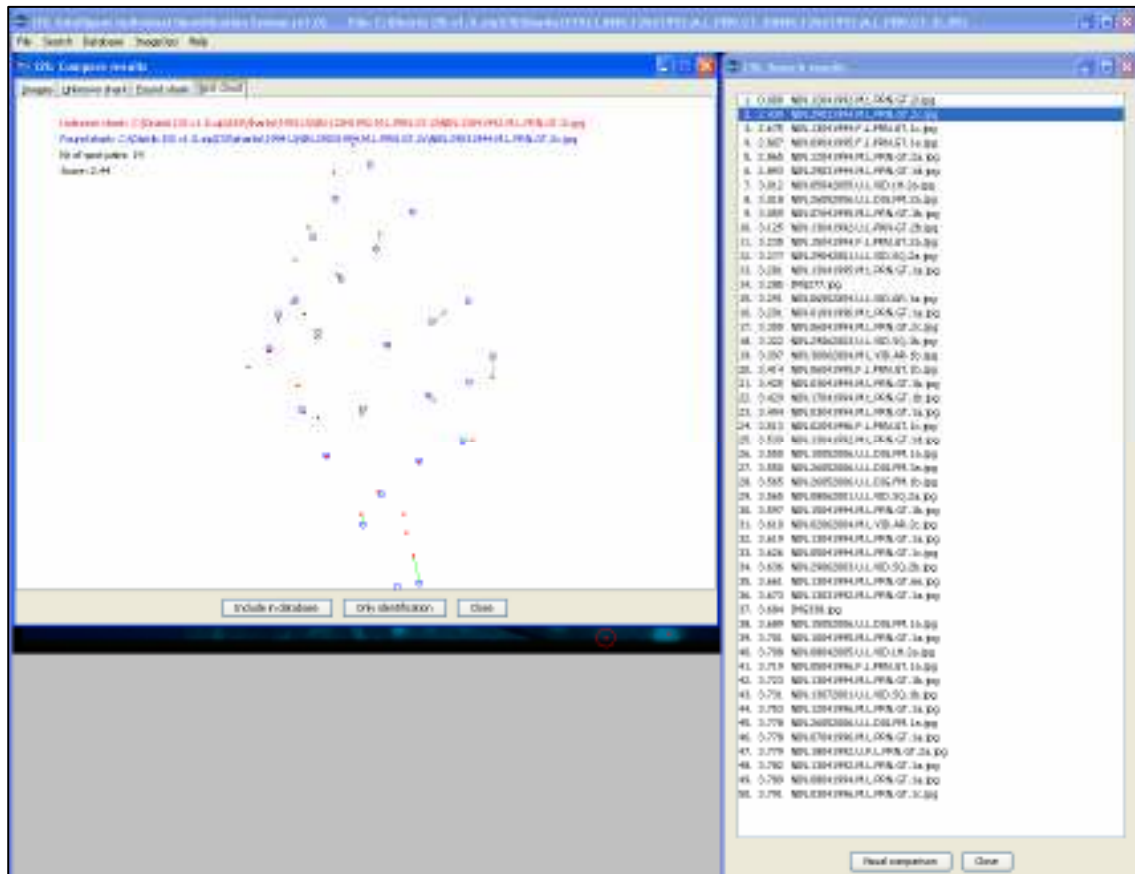


Figure 9. Spot cloud of matching spot pairs (left side of the screen). The red spots are the fingerprint from the unknown shark, and the blue spots are the fingerprint from a shark found in the database. The green lines denote the distance between match spot pairs.

I³S matching validation. *I³S* provides the user with a matching score, however; this score does not take into account the uncertainty in the system, nor does it provide a relative score to all other images considered. A non-subjective validation technique is essential to assess the relative strength of matches, which has not been provided to date for automated photo-identification studies. Without a validation of image matches, the final decision is subjective, and may affect the quality of data used for parameterisation of demographics.

To provide a measure of match parsimony based on the philosophy of information theory and to compare possible image matches in a multi-model inferential framework (Burnham and Anderson 2002), I modified the match score in the

following manner: (1) the spot-averaged sum of squares was back transformed to a residual sum of squares, which was simply the spot score (SS) multiplied by the square of the number of matching spots (n); (2) an information criterion (IC) analogous to the Akaike Information Criterion (Akaike 1973) was calculated as follows:

$$IC = 2k + n' \log_e \left(\frac{SS \cdot n^2}{n'} \right) \quad \text{Equation 3}$$

where k = an assumed number of parameters under a simple linear model (set to 1 for all models) and the $n' = 100/n$ and accounts for the fact that an increasing number of spots automatically leads to a higher SS (the 100 multiplier scales the term to be > 1);

(3) the IC weight (w) was calculated as:

$$w_i = \frac{e^{-0.5 \cdot \Delta IC_i}}{\sum_{i=1}^m \Delta IC_i} \quad \text{Equation 4}$$

where $\Delta IC = IC - IC_{min}$ for the i^{th} image (i^{th} 'model') 1 through m (where $m = 49$);

(4) finally, the evidence ratio (ER) was calculated as:

$$ER_1 = \frac{w_1}{w_2} \quad \text{Equation 5}$$

This IC algorithm was applied to a sample of 200 images; 25 matching pairs from the LS and RS databases and 25 non-matching pairs from the LS and RS databases. The LS and RS images were analysed separately using text outputs from I³S showing image name, I³S matching score and number of pairs matched by I³S (Appendix 1).

The analysis was done using the *R* Package (R Core Development Team 2004); the code for the IC algorithm, (including w and ER), is given in appendix 2.

Assessment of ‘by-eye’ matches using I³S. A by-eye comparison of images in the photo-library when it consisted of a total of 581 images (excluding images collected in 2001, 2005 & 2006), was done by a student in 2004. During analysis, photos were sorted into quality classes on the basis of clarity, angle, distinctiveness, partial image and overall quality (Friday *et al.* 2000; Meekan *et al.* 2006). Thirty-three individual sharks were resighted inter-annually during the manual by-eye analysis of the raw photo-library. Of any two by-eye matched images, one of the pair was entered into either the LS or RS I³S database and searched. A match using I³S was considered successful if the by-eye matched images were ranked in the 1st position using I³S and ‘validated’ using and the IC algorithm. From the results of the non-matching pairs in the validation experiment, I aimed to determine an IC w threshold below which matching certainty was low. An image was considered to be validated if it received an IC w score above this threshold.

Effect of horizontal angle on matching success. Images where whale sharks are on oblique horizontal angles to the camera are common in the database. It is possible that such images affect the matching ability of the linear algorithm used by I³S. Therefore, it was necessary to assess what effect these images have on matching success, to provide a horizontal angle limit, beyond which matching success was unlikely.

Five images of either the LS or RS of 10 sharks were captured from video footage at varying degrees (0, 10, 20, 30 and 40°) of yaw. (Fig.10). Angles of yaw were estimated on screen using Screen Protractor™ software (Fig.11). The bottom calliper was set to be horizontal to the camera, while the alternating calliper was lined up to be perpendicular with the base of the pectoral fin.

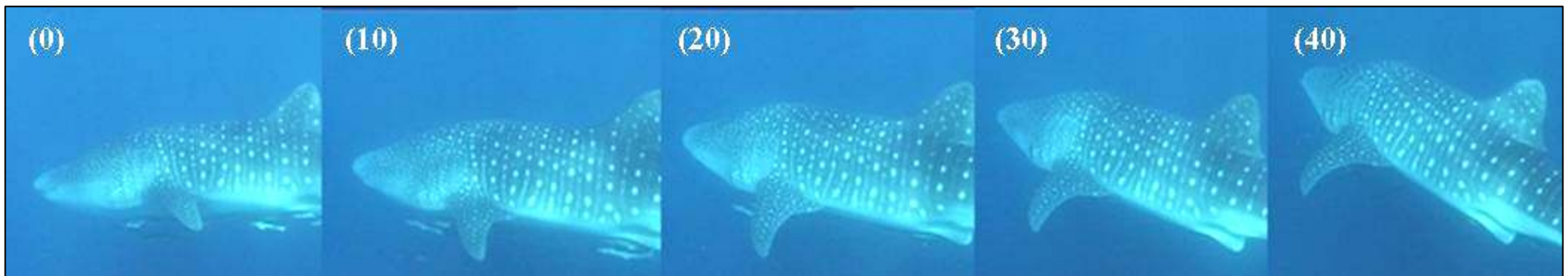


Figure 10. Five angles (0° , 10° , 20° , 30° and 40°) of an individual shark for angle comparison in I^3S .

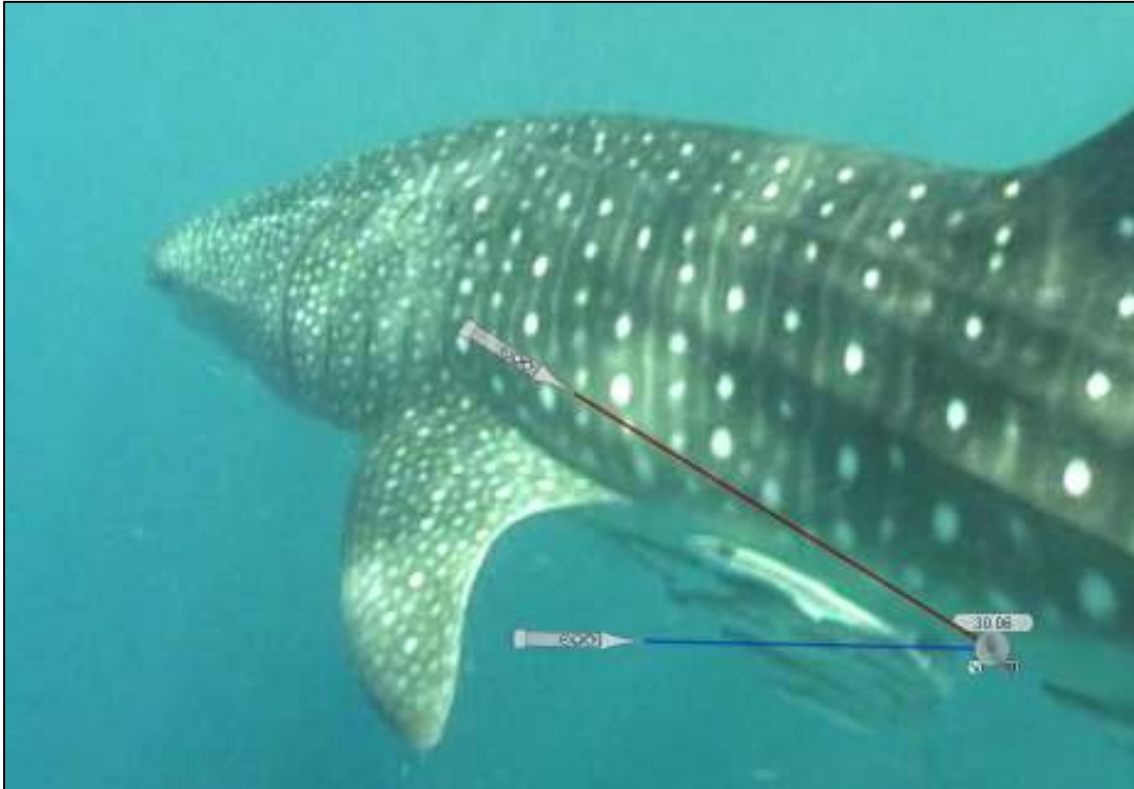


Figure 11. Horizontal angle measurement of a shark with Screen Protractor, showing a horizontal angle of approximately 30°.

Fingerprints were then created for each image using 20 spots per fingerprint. The 10° images were searched against the 0° images and 10 non-matching images. This process was repeated, substituting the 10° images where subjects were on angles of 20°, 30° and 40°, for both LS and RS image sequences.

Five random, non-matching pairs were also searched against 0° and 10° images, and then repeated for 20°, 30°, and 40° images. This allowed for a comparison between matching and non-matching pairs, while testing for the effects of horizontal angle in images. Results were analysed using the information criterion algorithm which was also applied to the match validation and by-eye comparison tests.

Assessment of the number of spot pairs compared. Based on the matching algorithm used by I³S, it was suspected that the number of matching spot pairs was affecting the I³S score. The IC algorithm developed takes the number of matching spot pairs into account, therefore I wanted to test whether a) there was a correlation between the I³S

score and matching spot pairs, or b) there was a correlation between IC w and ER scores and the number of matching spot pairs. To do this, fifty known matching pairs (25L & 25R) were compared with one another in I^3S . Of these matching pairs, pairs successfully confirmed during validation of I^3S matches only were included for assessment of spot number. I^3S scores were compared against the number of spot pairs matched. The w_1 for each image were also compared against the number of spot pairs matched by the I^3S algorithm. A complementary log-log function (clog-log) was applied to normalise the distribution for I^3S scores and w_1 , and a \log_{10} transformation was used to normalise the distribution of spot pairs. Finally, a linear regression was applied to determine whether there was a correlation between either I^3S scores and spot pairs, or w_1 and spot pairs.

Whale shark population size. The capture matrix used for the previous by-eye study of the whale shark population (Meekan *et al.* 2006) was constructed using the old system of individual naming, which no longer corresponded with the images and identified matches in the database. In addition, the previous capture matrix was based on images that were matched with unquantified human bias. The previous study also matched some individuals using other identifying features such as scarring. Therefore, I wanted to create: 1) a capture matrix for the whale shark database, where images were matched using I^3S , and 2) a capture matrix where only validated resights were included. This would remove some human error inherent in the system, while assist in strengthening population estimates. To achieve this, a new naming of individuals was necessary to construct the new capture matrix. The new individual identifier, analogous to the naming convention used for individual photographs, included a unique number, the sex of the animal and which side of the animal had been photographed during the course of its resight history:

WS00001MB

This individual is number one (00001), it is male (M) and it has had both left and right sides photographed (B) during the course of its resighting history. If this individual had only the left side photographed, the identifier would read: WS00001ML.

The initial population size estimates for this study were calculated using the capture matrix based on I³S matches. The capture matrix consisted of all individuals with both sides fingerprinted, and RS only fingerprinted. Individuals which had LS fingerprinted only, were excluded to reduce the potential error of double counting. Only inter-annual sightings of individuals were included within the capture matrix. Population size estimates were further refined by repeating the experiment using the capture matrix consisting of only I³S matches that had been validated using the IC algorithm. Images that received IC *w* scores above the IC *w* threshold were considered to be validated. All resights that were not validated were removed from the capture matrix prior to reanalysis. Similarly, this capture matrix only consisted of inter-annual sightings of individuals.

Population estimates using a series of closed population models (assuming no net immigration or emigration) were initially calculated using the program CAPTURE, and examined variants of the Lincoln-Petersen (LP) model (Meekan *et al.* 2006). Due to the sensitivity LP estimates to temporary emigration and the low power associated with databases comprising a low rate of recapture (resighting), I also considered an open-population Cormack-Jolly-Seber model (Schwarz and Arnason 1996) using the POPAN option in the program MARK (White and Burnham 1999) to estimate population abundance (Table 1).

Table 1. Open-population models for whale shark population re-assessment using MARK

Model Name	Model Equation
<i>Constant (null)</i>	$\phi(.)p(.)\beta(.)N(.)$
<i>Capture probability-time variant</i>	$\phi(.)p(t)\beta(.)N(.)$
<i>Apparent survival-time variant</i>	$\phi(t)p(.)\beta(.)N(.)$
<i>Probability of entry-time variant</i>	$\phi(.)p(.)\beta(t)N(.)$

*Note. ϕ = apparent survival, p = capture probability, β = probability of entry to population per occasion and N = super-population size.

Time intervals were set according to years sampled between 1992 and 2006 which were yearly from 1992-1996, 2001, then again yearly from 2003-2006). As such, the number of years elapsed between resighting events (years) was 1, 1, 1, 1, 5, 2, 1, 1 and 1. All models were fitted using the logit link function for ϕ and p , the identity link function for N , and the multinomial logit link function (MLogit [1]) to constrain the β parameters to be ≤ 1 (White and Burnham 1999). Parameters counts (k) for each model were adjusted to account for the fact that not all were estimable due to low recovery rates in some years. Akaike's Information Criterion corrected for small sample sizes (AIC_c) was adopted to give a model comparison and model-averaged estimates of N (Burnham and Anderson 2002). AIC_c was calculated as follows:

$$AIC_c = -2 \log L + 2k + \frac{2k(k+1)}{n-k-1} \quad \text{Equation 6}$$

Goodness-of-fit was calculated using the program Release GOF. The coefficient of variation (CV) was also calculated for each model as a measure of parameter precision for abundance estimates:

$$CV = \frac{Sd}{\chi} \times 100 \quad \text{Equation 7}$$

Results

I³S matching validation. The information criterion weights (w) for the most parsimonious match (w_1) for the 50 matched pairs were broadly distributed between 0.05 and 0.85, while w_1 for non-matched pairs were highly right-skewed (12a & 12b). All w_1 for non-matched pairs were < 0.18 . The median w_1 for matched pairs was 0.32 (\pm SE 0.05), which was much higher than the median for non-matched pairs 0.06 (SE \pm 0.01). Evidence ratios (ER) for the best-matched relative to the next-highest matched images (ER_1) for known matched pairs were also highly right skewed and ranged from 0.73 to 51.92, with a median of 7.36 (\pm 2.45) (Fig.12c). ER_1 values for non-matched pairs were all < 3.5 (median = 1.21 \pm 0.09) (Fig.12d). Evidence ratios for the second best-matched relative to the next-highest matched images (ER_2) for known matched pairs ranged from 0.73 to 114.18, with a median of 7.57 (\pm 3.82). ER_2 values for non-matched pairs were also < 3.5 (median=1.42 \pm 0.12).

Overall, 93 % of the 100 I^3S -matched images were assigned correctly using the IC w and ER . IC w_1 for the correctly assigned matches ranged from 0.05 to 0.85 (median = 0.36 \pm 0.04), and their ER_1 ranged from 0.73 to 51.92 (median = 8.82 \pm 2.56) (Fig.13 Figure 13a & 13b). Incorrectly assigned matches had IC w_1 that ranged from 0.05 to 0.14 (median = 0.07 \pm 0.07), with their ER_1 ranging from 0.95 to 2.28 (median = 1.23 \pm 0.35).

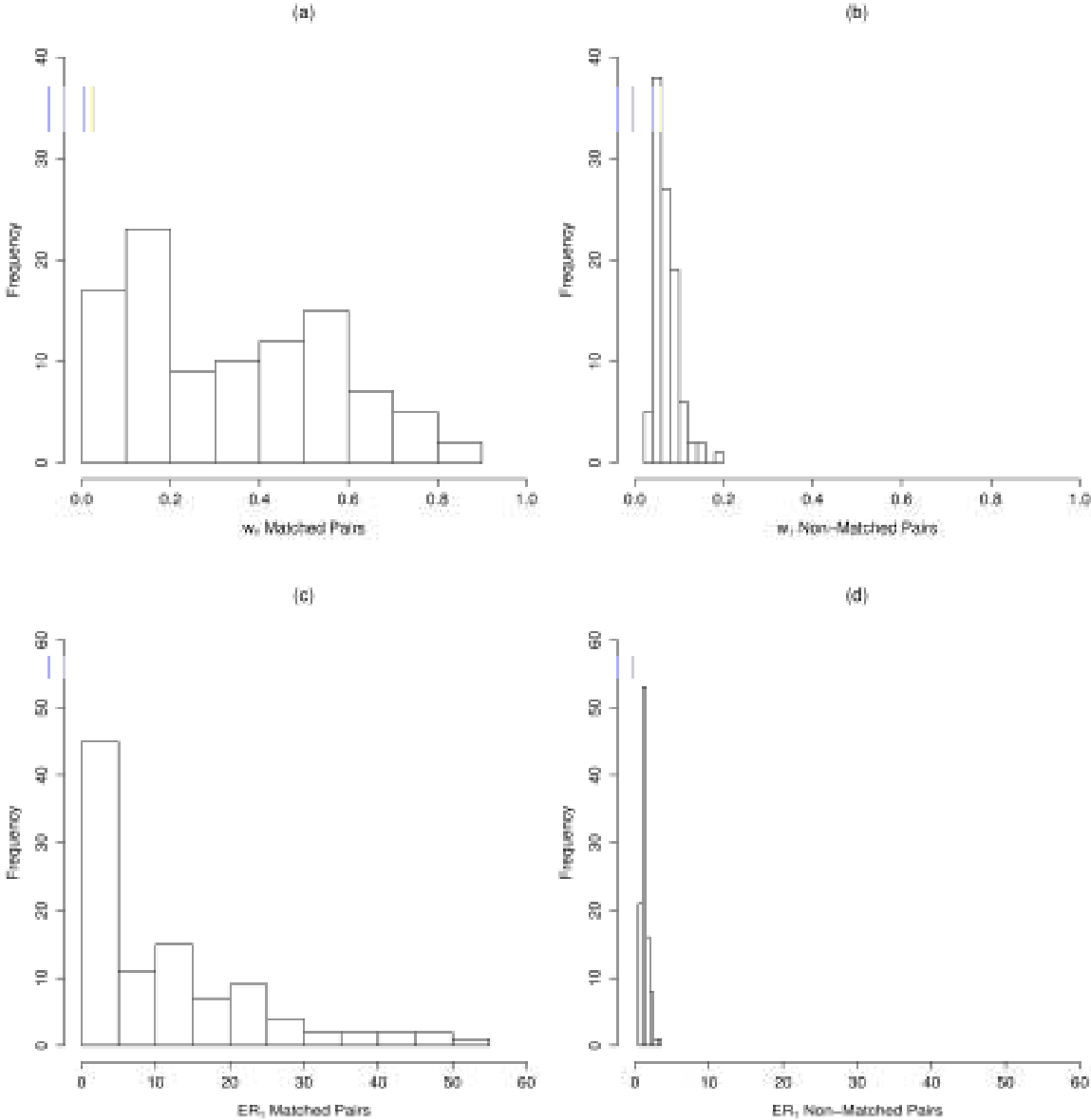


Figure 12. I³S matching validation IC weights (w_l) for known matched (a) and non-matched pairs (b), and I³S matching validation evidence ratios (ER_l) for known matched (c) and non-matched pairs (d).

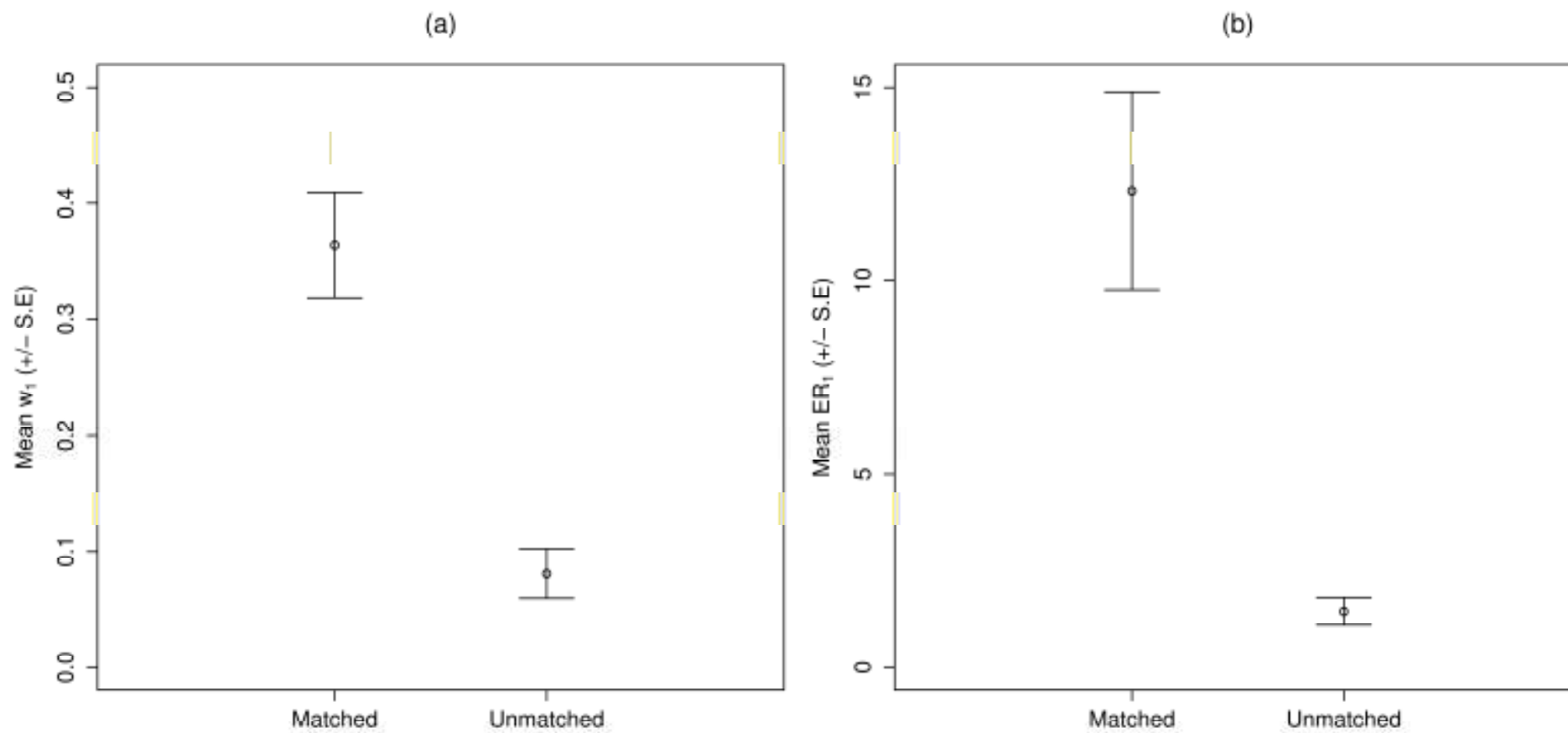


Figure 13. Mean (a) IC weights (w_l) for known matching pairs showing validated and non-validated matches; (b) Mean evidence ratios (ER_l) for known matching pairs showing validated and non-validated matches.

Assessment of 'by-eye' matches using I³S. Of the 33 individuals resighted between years in the database used by Meekan *et al.* (2006), 10 individuals could not be matched with I³S because their images were not amenable to I³S fingerprinting (absence of reference points) or their match was not present in the database. This was because the Meekan *et al.* (2006) study also used images from a separate database and included scar-identified individuals that were not available for photographic matching using I³S. Thus, we could only re-assess 23 of these by-eye matches that included 13 left side (LS) matches and 16 right side (RS) matches (58 images total).

Forty-eight of the 58 images (83 %) were assigned correctly using the w and ER . w_1 for the correctly assigned by-eye matches ranged from 0.05 to 0.53 (median = 0.16 ± 0.04) (Fig.14a), and their ER_1 were between 1.04 and 24.57 median = 2.33 ± 1.60) (Fig.14b). Incorrectly assigned by-eye matches had w_1 ranging from 0.04 to 0.13 (median = 0.05 ± 0.02) and ER_1 0.67 to 2.76 (median = 1.04 ± 0.38). ER_2 scores for correctly assigned images ranged from 1.05 to 28.07 (median = 3.99 ± 1.80). Incorrectly assigned by-eye matches had ER_2 ranging from 0.99 to 4.07 (median = 1.29 ± 0.59).

I³S also identified two false-positives images matches which were not detected in the by-eye matching process. Neither of these images was matched with other known images of the identified sharks. Upon closer manual inspection, I determined that these images were from different sharks.

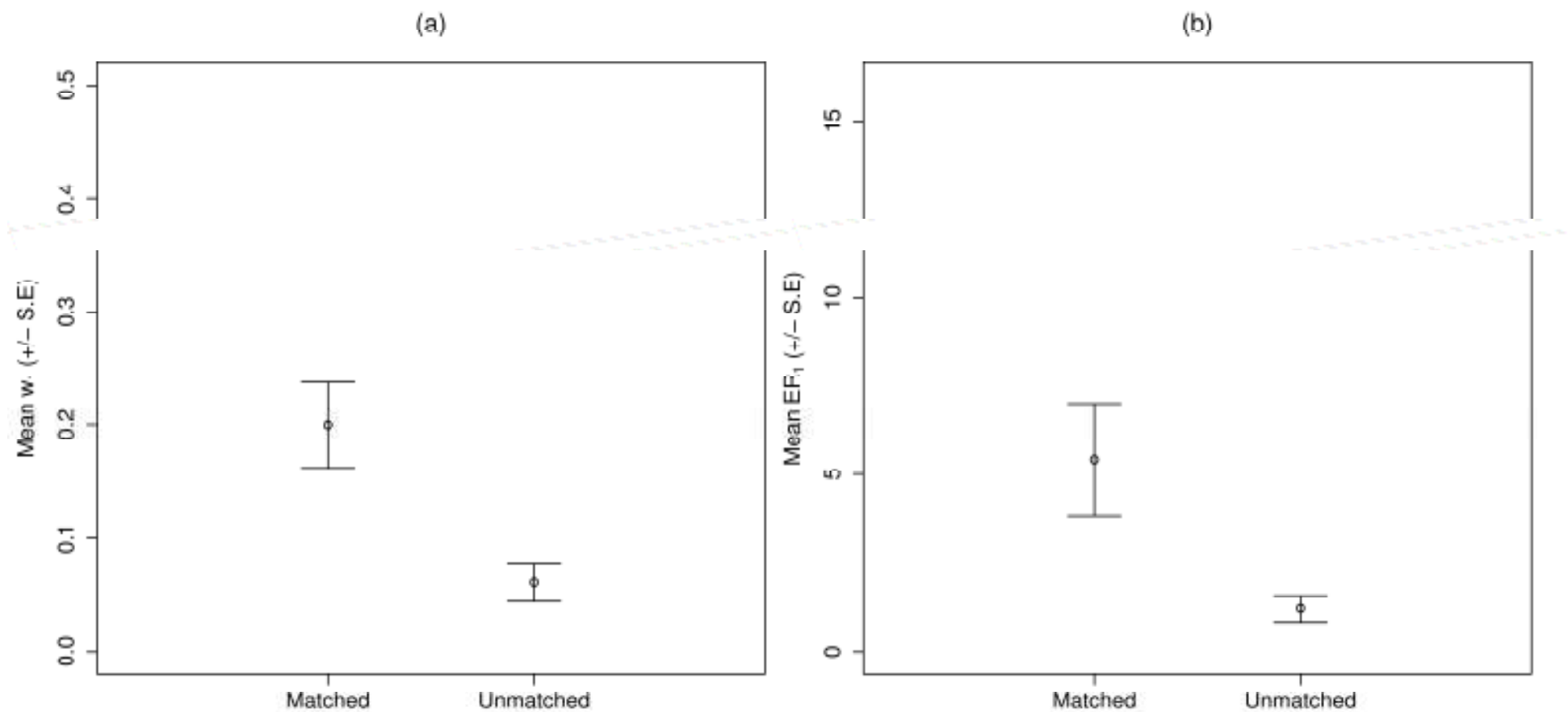


Figure 14. (a) Mean IC weights (w_l) for known matching pairs showing validated by-eye matches and non-validated by-eye matches; (b) Mean evidence ratios (ER_l) for known matching pairs showing validated by-eye matches and non-validated by-eye matches.

Testing the effect of horizontal angle on the matching success of I^3S . Mean w_1 decreased linearly as the horizontal angle of subjects within images increased (Fig.15a). Mean w_1 ranged from 0.88 (± 0.06) for angles of 10°, to 0.30 (± 0.13) for angles of 40°. S.E for w_1 were relatively low for angles of 10° and 20°; however, increased for angles of 30° and 40°. The images of subjects at 30° angles approached mean w_1 for non-matching pairs, and mean w_1 for images of subjects at 40° overlapped mean w_1 for non-matching pairs.

There was an exponential decline of mean ER_1 from the 10° category to the 20°, 30° and 40° categories (Fig.15b). Mean ER_1 ranged from 89.42 (± 52.23) for images of subjects at 10° to 4.06 (± 2.80) for images of subjects at 40°. There was also an exponential decrease in standard errors from images of subjects at 10° to images of subjects at 20°, 30° and 40°. The images of subjects at 30° angles approached mean ER_1 for non-matching pairs, and mean ER_1 for images of subjects at 40° overlapped mean ER_1 for non-matching pairs.

Assessment of Spot #. I^3S scores and spot pairs, and w_1 and spot pairs showed a greater degree of normality and better residuals after data transformation. A strong correlation ($ER = 9.94 \times 10^5$; adjusted $R^2 = 0.26$) was observed between the complementary log-log transformation (clog-log, to normalise proportions) of I^3S scores and the \log_{10} -transformed number of spot pairs (Fig.16a). No correlation was observed between clog-log w_1 and the \log_{10} number of spot pairs (Fig.16b).

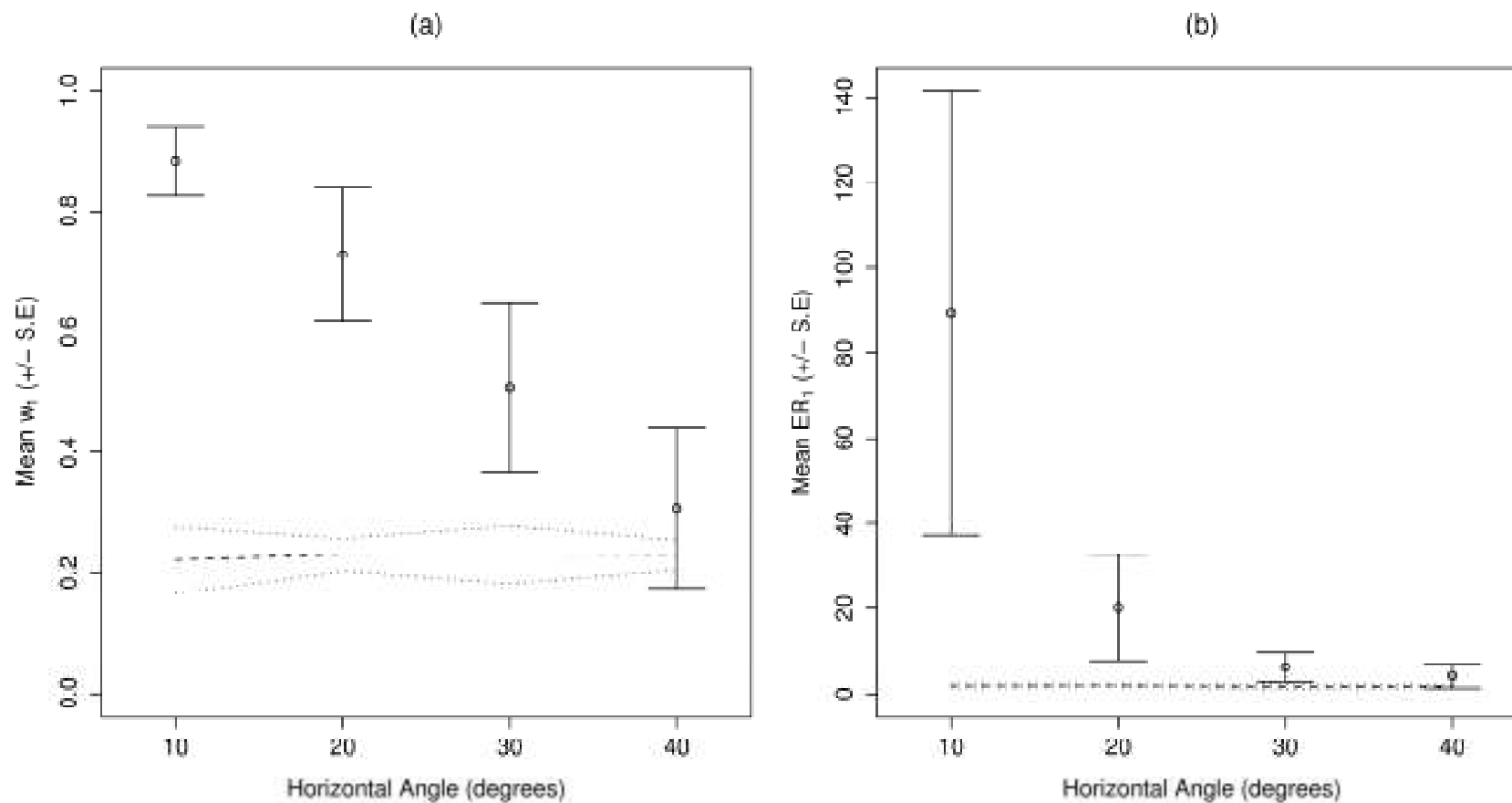


Figure 15. (a) Mean IC weights (w_l) for horizontal angle categories, where images at 0° were matched against images skewed by 10, 20, 30 and 40° . Dotted lines show results for non-matching pairs; (b) Mean evidence ratios (ER_l) for horizontal angle categories, where images at 0° were matched against images skewed by 10, 20, 30 and 40° .

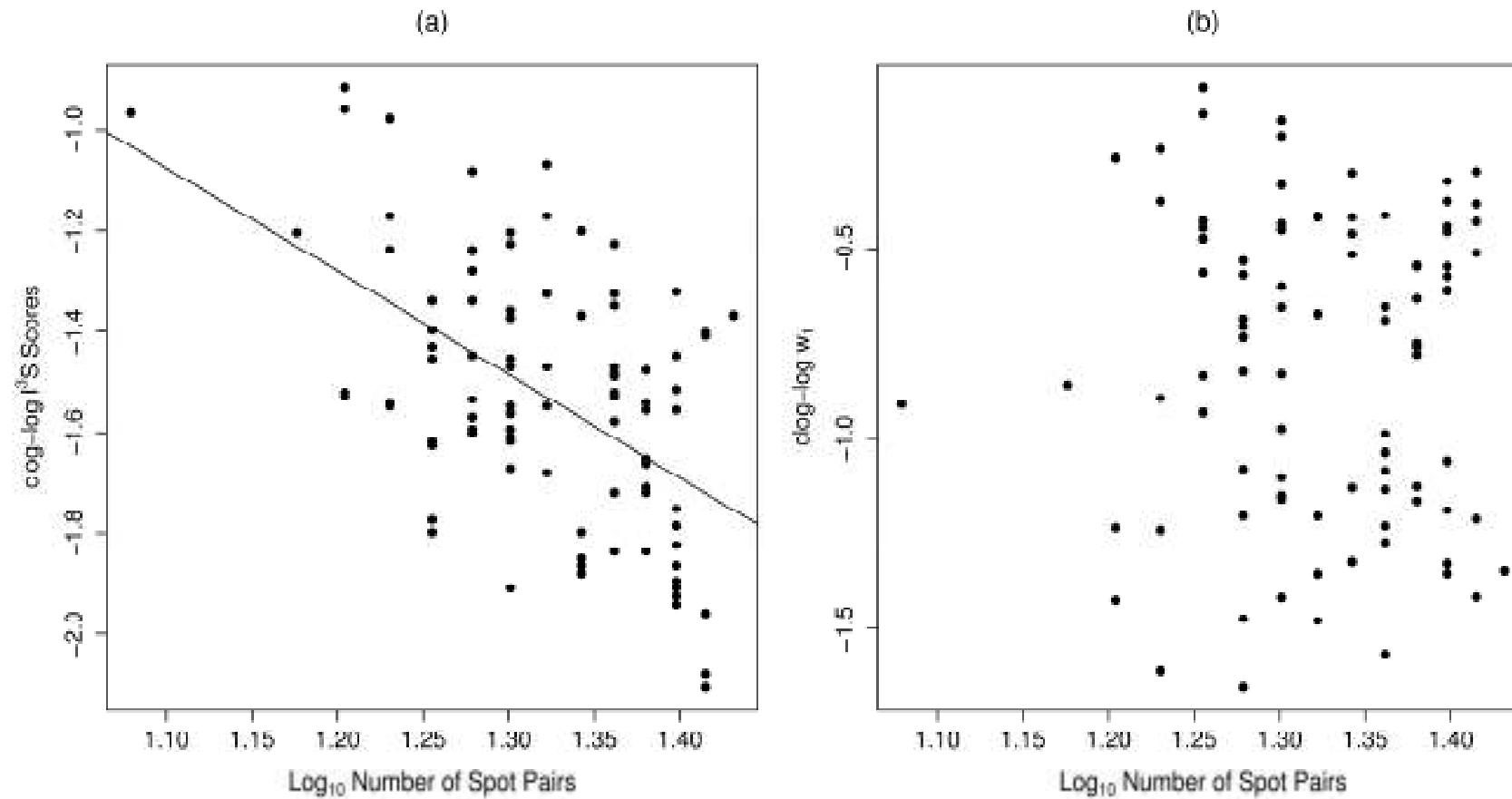


Figure 16. (a) Relationship between complementary log-log-transformed (clog-log) $\hat{I}^3\text{S}$ scores and log_{10} -transformed number of spot pairs. The fitted line illustrates the correlation observed using a linear regression; (b) Comparison of clog-log-transformed w_l with log_{10} -transformed number of spot pairs.

Whale shark population size using I^3S matches. After the removal of multiple images of the same individual, a total number of 208 individual sharks were identified for the period between 1992 and 2006 (excluding 1997, 1998, 1999, 2000 and 2002). Eighty-four of these individuals had both RS and LS fingerprints, 73 had RS fingerprints only and 51 had LS fingerprints only. I therefore excluded individuals with LS only fingerprints to avoid double counting the same individual, which left a total of 157 individuals suitable for use in population estimates. From a total of 157 individuals, there were 30 individuals that were resighted inter-annually. Twenty-six of these were included in the population analysis as they either had the right side or both sides fingerprinted.

Ten capture sessions (excluding years where sampling did not occur) including 157 individuals with fingerprints, seen in 187 separate sightings over the study period, enabled the estimation of population size using differing models and estimators. The model that provided the best fit under the model selection criteria provided by CAPTURE was the time-variant and heterogeneity model (M_{th} , model selection criterion = 1.0). Tests for closure ($z = -1.886$, $P = 0.029$) and closure by frequency of capture ($z = -3.825$, $P = 0.00007$) both violated the assumption of homogeneity of capture probabilities (i.e., the population was not closed). The M_{th} model using the Chao estimator provided time-variant capture probabilities (p_t) ranging between 0.01 (2005) and 0.08 (1994). No trend was observed over time. Population estimates are summarised in (Table 2).

Table 2. Summary of population size estimates from closed and open populations for I³S resights

Model	Goodness of Fit		N Range	CV (%)
Closed				
M_{th} (1992-2006)			367-780	20
M_{tb} (1992-2006)	Chao	$\chi^2_7 = 34.64$ $P = <0.001$	189-5216	150
M_t	Chao	$\chi^2_{58} = 71.95$ $P = 0.102$	347-628	15.5
Open (Jolly Seber)				
$\phi(.)p(.)\beta(.)N(.)$		$\chi^2_1 = 0.28$ $P = 0.60$	265-363	8.2
$\phi(.)p(.)\beta(t)N(.)$		$\chi^2_1 = 0.28$ $P = 0.60$	265-363	8.2

*Note. ϕ = apparent survival, p = capture probability, β = probability of entry to population per occasion and N = super-population size.

Only one of the parameters for time-variant models converged using the POPAN open-population Jolly-Seber model structure, which was the time-variant probability of entry model ($\phi(.)p(.)\beta(t)N(.)$). The reason that many of the time variant models did not converge was due to some parameters being inestimable from a low number of resights in particular years. The constant model ($\phi(.)p(.)\beta(.)N(.)$) converged with an AIC_c of approximately 100 % (Table 3) and provided a super-population size of 265-363 individuals (Table 2).

Table 3. Results for model analysis using non-validated (unvalidated) I³S dataset - Small sample size corrected Akaike Information Criterion (AIC_c), Delta AIC_c (Δ AIC_c), AIC weights (w AIC_c), number of parameters (NP) and Deviance.

Model	AIC _c	Δ AIC _c	w AIC _c	NP	Deviance
$\phi(.)p(.)\beta(.)N(.)$	16252.9491	0.0000	0.99841	3	15420.6390
$\phi(.)p(.)\beta(t)N(.)$	16265	12.8868	0.00159	9	15420.6390

Whale shark population size using validated I^3S matches. Using the w_1 threshold of 0.2 determined from the validation tests, only 14 of the 26 individuals resighted inter-annually were validated. w_1 for validated resights ranged between 0.21 and 0.77, with a mean of 0.41 (S.E \pm 0.08) (Fig.17). w_1 for non-validated (unvalidated) resights ranged between 0.05 and 0.14, with a mean of 0.06 (S.E \pm 0.02).

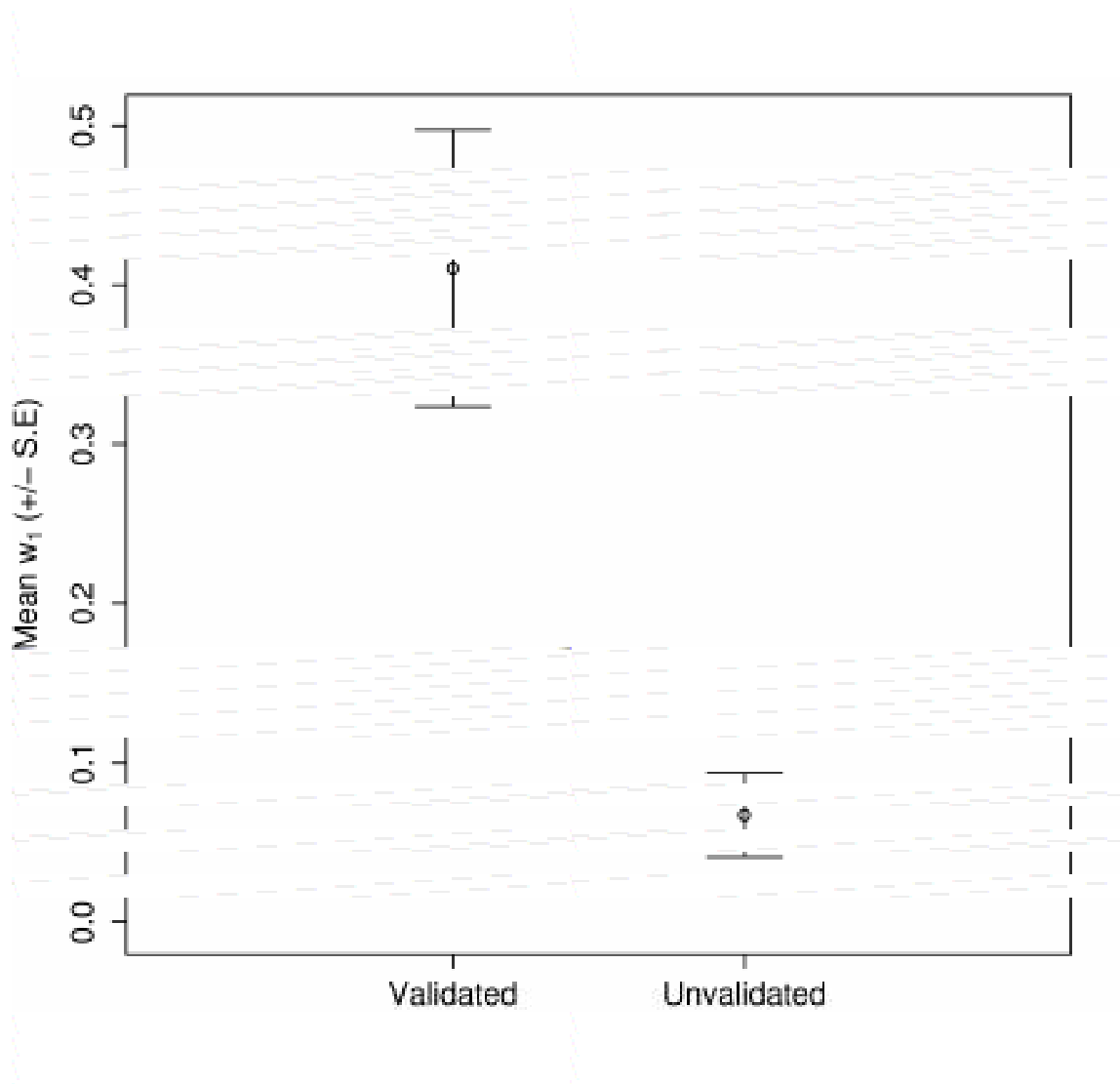


Figure 17. Mean validated and unvalidated (< 0.2) w_1 for inter-annual resights used for population modelling.

The ten capture sessions included 145 individuals with fingerprints seen in 161 separate sightings over the study period. These were used to create IC-validated population estimates using differing models and estimators. The model which provided the best fit under the model selection criteria provided by CAPTURE, was

the time variant model (M_t) ($\chi^2_{56} = 58$, $P = 0.40$, model selection criterion = 1.0) (Table 4).

The test for closure ($z = -2.783$, $P = 0.002$) and closure by frequency ($z = -3.525$, $P = 0.00021$) were both violated under the null model of no heterogeneity in capture probabilities. The M_t model using the Chao estimator provided time-variant capture probabilities (p_t) ranging between 0.01 (1993) and 0.05 (1994). No trend was observed over time. Population estimates are summarised in table 4.

Table 4. Summary of population size estimates from closed and open populations for validated \hat{I}^3S resights

Model		Goodness of Fit	N Range	CV (%)
Closed				
M_t (1992-2006)	Chao	$\chi^2_{56} = 58$ $P = 0.40$	447-1211	26.2
M_{tb} (1992-2006)	Chao	$\chi^2_7 = 27.74$ $P = < 0.001$	176-8696	203
M_{th} (1992-2006)			497-1428	28
Open (Jolly Seber)				
$\phi(.)p(.)\beta(.)N(.)$			280-453	12.4
$\phi(.)p(.)\beta(t)N(.)$			280-453	12.4

The only time-variant model with converging parameters was the time-variant probability of entry model. The constant model using the POPAN open-population Jolly-Seber model structure implemented in MARK for 1992-2004 estimated the super-population size at between 280 and 452 individuals, with an AIC_c of approximately 90 % (Table 5).

Table 5. Results for model analysis using validated I³S dataset - Small sample size corrected Akaike Information Criterion (AIC_c), Delta AIC_c (Δ AIC_c), AIC weights (w AIC_c), number of parameters (NP) and Deviance.

Model	AIC _c	Δ AIC _c	w AIC _c	NP	Deviance
$\phi(.)p(.)\beta(.)N(.)$	11517.4869	0.0000	0.89255	3	10803.5630
$\phi(.)p(.)\beta(t)N(.)$	11521.7211	4.2342	0.10745	5	10803.5630

Discussion

Consistent, non-intrusive and ethically acceptable methods of capture-mark-recapture are essential for estimating reliable demographic rates for wildlife populations, particularly for threatened species (Fagan and Holmes 2006). Photo-identification has become a widely accepted method of capture-mark-recapture that has been empirically tested over a wide range of fauna (e.g. Dixon 2003, Fujiwara and Caswell 2001, Karanth and Nichols 1998). Despite the advantages of this technique, there is the potential for users manipulating large photographic databases to compromise the reliability of matches made by eye, which can subsequently jeopardise estimates of population abundance and vital rates. This problem has been largely overcome for several species by computer-aided image-matching algorithms that match various unique features of individuals (e.g., Kelly 2001, Kehtarnavaz *et al.* 2003, Gope *et al.* 2005, Karlsson *et al.* 2005 and Arzoumanian *et al.* 2005). However, many of these programs have limited applications, may be complex to operate, or are not freely available to the large body of potential (non-technical) users.

Software inaccessibility and the corresponding isolation of potentially useful photographic datasets will likely compromise parameter estimation and lead to higher uncertainty in estimated vital rates. For example, centralised photographic catalogues are common in the field of cetacean research, with new photographs from observers being compared to those previously obtained and the results sent to collaborators around the world (Agler 1992). This type of data sharing for large, long-lived and wide-ranging species is an essential component of effective population management. This is because limited sampling both in space and time may not provide enough data to accurately represent population structure, trends and stochastic elements which may regulate demographic processes. Open-source matching software coupled with matching algorithms exploiting the power of information theory will make obtaining adequate demographic information more efficient and less error prone.

My assessment of a simple, freely available spot pattern-matching software Interactive Individual Identification System (I³S), coupled with an information-theoretic incorporation of matching uncertainty has shown to be particularly effective for whale sharks, given their natural spot patterns were ideally suited for assessment

using the I³S software. Validation of I³S matches using the information criterion algorithm provided an information criteria weight threshold for known matched pairs of approximately 0.2, below which information criteria weights for non-matched pairs fell. Known matched pairs unsuccessfully matched by I³S or that were matched with low (i.e., < 0.2) information criteria weights likely resulted from poor clarity or high angles of yaw (Fig.18 a-f). Images 'c' & 'd' may have also been affected by pitch and roll, as image 'd' was taken at a considerably lower vantage point than 'c'.

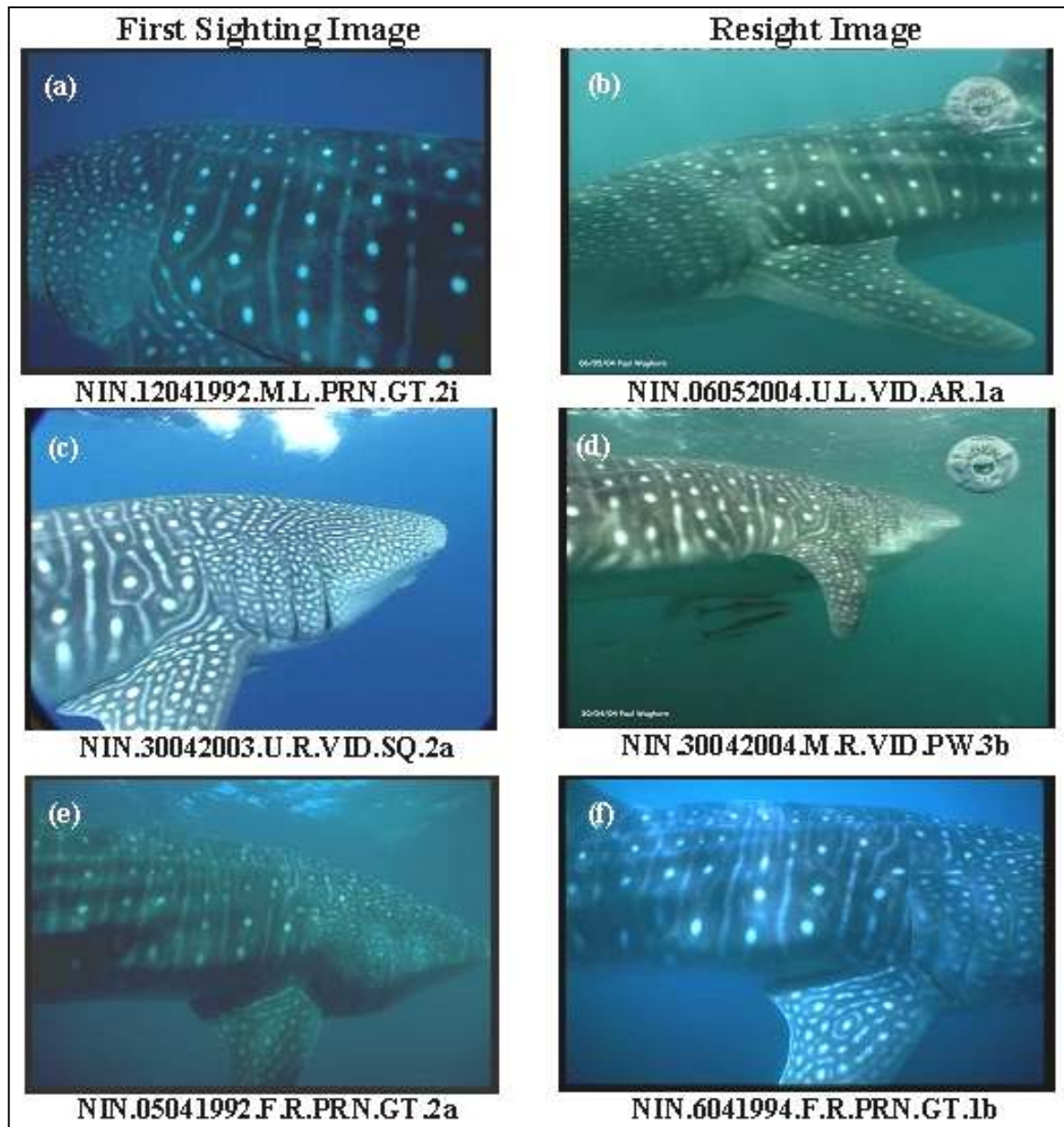


Figure 18. Known-matching images that were not matched with I³S or validated.

Non-matching evidence ratios fell below 3.5, providing an analogous threshold to that derived using information criteria weights. Known-matched images that fell below the evidence ratio threshold scored badly due to the same image problems which resulted in low information criteria weights (Fig.18), however; unlike information criteria weights which are relative to all images considered, evidence ratios are only relative to the next ratio above it and therefore if ER_1 is low, ER_2 should also be examined as a possible match. This emphasises the need to select images of the highest 'quality' for matching purposes. Ideal photos for use with I³S should be clear, and the subject should not be flexing or on an oblique angle to the camera.

The validation process is necessary with most computer-aided matching algorithms because this alleviates much of the subjectivity associated with the final stage of matching. The validation technique developed in this study is unique, and for the first time provides researchers who use photo-identification with a non-subjective means of confirming image matches based on match quality. It is advisable for other researchers using photo-identification to assess their image matches using this validation technique, and I encourage the incorporation of this technique into standard protocol when matching images. In the case of whale sharks, the 0.2 threshold proved to be a robust and conservative measure of match certainty. This threshold is likely to vary depending on the size of the area which is restricted by the reference points, ergo the number of potential matching pairs, which may in turn result in different information criteria weight thresholds for other animals (Hartog pers. Com.). Nonetheless, in the absence of validation data I suggest that using this threshold value is a good first approximation. This is because the requirement for the top ranked image to be above the threshold is a conservative estimate of match certainty, likely to hold true for other organism with similar patterns.

The validation stage of photographic matching can be further confirmed by using genetic tagging to identify individuals (Stevick *et al.* 2001), which may become feasible for iconic species such as the whale shark. Genetic tagging also has the added advantage of providing additional individual- and population-level information (e.g., genetic diversity, parent-offspring relationships, etc.) (Palsboll 1999). However, genetic tagging for capture-mark-recapture purposes is not without its problems. This technique cannot differentiate between correctly and incorrectly read marks because

the number of genome types (marks) in a population is unknown, the genome used for id may not provide a unique mark, and sampling occasions may be problematic when using non-intrusive sampling methods (Lukacs and Burnham 2005). Any of the aforementioned issues have the potential to affect capture-mark-recapture estimates in a similar fashion to the misidentification of individuals from photo-id or traditional tagging. Because whale sharks are frequently photographed and tissue sampling may be difficult and expensive to process, it is unlikely that genetic tagging will replace photographic identification in the near future. However, additional validation will allow improvements of initial estimates of the population size and survival probability for the effective management of the whale shark population at Ningaloo Reef (Meekan *et al.* 2006) and elsewhere.

The open-source program I³S was effective at confirming past matches made by eye in the majority of instances. Images that were successfully confirmed using the information criteria algorithm received relatively low mean information criteria weights and evidence ratios overall, most likely as a result of a considerably smaller sample size than that used for validation. I³S was also a useful tool for identifying image matches that were assigned incorrectly (i.e., both false positives and false negatives). When matching whale shark patterns by eye, the observer generally does not focus on the spot pattern *per se*; rather, attention is usually paid to the intricate lines and whirls on the flank of the shark (Fig. 1a). As such, I³S provides an unbiased method of matching natural markings that is relatively immune to user subjectivity.

I found strong evidence that horizontal angle of subjects within images affects the ability of the I³S algorithm to make reliable matches. As the horizontal angle of subjects in images increases, the matching likelihood decreases. Angles of yaw up to 30 ° compromise the matching process even though many of these images were still matched correctly, which highlights the importance of visual validation of information criteria close to the threshold. Images with angles of yaw $\geq 40^\circ$ however, will more than likely be incorrectly assigned. Information criteria weights and evidence ratios were relatively high in comparison to those obtained in the validation test. This was most likely due to the fact that the images used for the horizontal angle test were compared against other images taken from the same piece of footage, where

individuals were situated in a constant orientation to one another. When matching images taken at different sightings, it is unlikely that the camera will be at exactly the same orientation each time; therefore, matching scores are likely to be negatively affected accordingly. Due to the linear algorithm used by I³S to match spot patterns, it is important to use only those photos with as little contortion of the reference area as possible. This is because when the position of spot pairs changes in relation to the reference points, the system may become unreliable (Hartog pers. com.).

The number of spots annotated in fingerprints can also potentially affect the I³S matching process. The higher the number of spot pairs matched, the lower the I³S score and hence, the higher the matching certainty. This relationship emphasises the benefit of using information-theoretic measures of matching parsimony because the updated algorithm takes into account the number spot pair used. The information criteria weights and evidence ratios for potential matches provide an unbiased score, for the range of spot pair numbers tested, which is resistant to differences in the number of matching spot pairs, and therefore, in the number of spots initially annotated during the fingerprinting process.

The number of suitable images from the whale shark database for use in I³S was considerably reduced when suitable reference points could not be identified, when image quality was poor and when subjects were at oblique angles to the photographer. The efficiency and reliability of matching with I³S however; more than compensated for the reduced sample size. Additionally, the number and size of images in an I³S database can potentially slow down the program's operating speed; therefore, it is ideal to scale down the size of photographs and only include the best image of a particular animal. In addition to horizontal angle, roll and pitch of subjects in images may affect the matching process. Pitch seems likely to be only a minor problem because digital photos can be rotated so that the animal is aligned with the horizontal. I had few images of the same individual at varying angles of roll, so I was unable to test the magnitude of this potential bias. There are, however; numerous images in the database of individuals taken at various different angles of pitch, which more than likely have a negative effect on the matching process.

Using permanent natural markings is the most ideal feature to use for photo-identification of individuals for capture-mark-recapture purposes (Pennycuik 1978 and Domeier and Nasby-Lucas 2006), because unlike many scars, natural markings do not change in appearance or multiply over time. Scarring may be useful for identification of some individuals as a form of double tagging, or validation of identification. Many individuals in the whale shark database bare scars or markings, which assisted in the identification of individuals in the previous by-eye study (Meekan *et al.* 2006). Unfortunately it is currently not possible to incorporate scars into the search function of I³S, which could narrow the search of individuals and potentially reduce search time for large image libraries. At this stage it is not possible to incorporate any other identifying feature of an individual into the search function in I³S that may assist in the matching process.

I split the I³S image library into left side and right side databases due to the fact that the program is not designed to distinguish between left side and right side images and therefore, running the search function with both left side and right side images in one database would have lead to many spurious matches. Swapping between databases to check left side and right side images of an individual can be time consuming, and is not ideal. Separating data for individuals into left and right side databases increases the risk of double counting the same individual as 2 different individuals (false negative). This can have serious implications to demographic estimates, such as an over estimation of population size.

Because the search algorithm in I³S is a two-dimensional linear algorithm, it is not only images taken at oblique angles to the camera that may negatively affect the matching process, but also images where an individual is flexing (Van Tienhoven *et al.* 2007). This potential problem is largely overcome for photo-identification of whale sharks because the area selected has little contortion during the undulation of the caudal fin. For other animals that have considerable contortion of the photo-identification reference area, individual identification using I³S could be problematic. Although, in this situation scarring or some other individual identifying mark may assist with image matching to some extent (Van Tienhoven *et al.* 2007), provided that the amount of contortion is nominal.

According to Van Tienhoven *et al.* (2007) the key feature of I³S is that it is not fully automated, and relies on the operator to discern between what is the natural pattern of the animal and what is an image artefact such as light refraction or backscatter.

Ironically, this feature is also one of the limitations of I³S. The system outlined by Arzoumanian *et al.* (2005) is mostly automated, and while matching of large sets of images may be less accurate than I³S, it is more time efficient. Nevertheless, the reliance of an algorithm to match patterns will always be inferior to the ability of the human brain to recognise complex spatial patterns, and therefore complete automation of image matching is not recommended. Therefore, the use of I³S in conjunction with the information criterion algorithm provides an ideal balance between user input and automation, which takes full advantage of human and software strengths for pattern matching.

Due to image quality issues such as horizontal angle, roll or flexing of subjects, the information criteria algorithm may be affected negatively and provide information criteria weights for known matches that are below the validated threshold of 0.2. This can be problematic for large image libraries and result in missing (unknown) matches, as well as require manual validation for known matches with near-threshold values of information criteria weights. Additionally, the user range of this validation technique may be limited in its present state because of the non-integration of I³S and the IC algorithm. While the process of obtaining information criteria weights and evidence ratios is not particularly difficult, it requires the user have a working knowledge of an object-oriented programming language such as the R Package (R Core Development Team 2004).

I³S applications

The application of I³S to any animal with a unique, stable spot pattern holds particular promise. The program is particularly well suited to organisms with > 12 spots within a defined and consistently identifiable reference area that are relatively homogenous in diameter and size. Large, irregular spots may cause problems during fingerprinting because the centre of the spot may vary according to the user's preference. Although, future versions of I³S may be able to accommodate for varying shaped spot patterns (Hartog. pers. com.). Aside from this study, the only species for which I³S has been empirically tested is the grey nurse, or 'ragged-tooth' shark (*Carcharias taurus*) (Van

Tienhoven et al. 2007). Another species of elasmobranch with a spot pattern that may be well suited to I³S is the white spotted eagle ray (*Aetobatus narinari*), which has an evenly spaced, relatively homogenous spot pattern on the dorsal surface (Fig.19A). Other species of rays such as the manta ray (*Manta birostris*) may not lend themselves as readily to I³S matching due to its large, sparsely spaced and irregular ventral spot pattern (Last and Stevens 1994) (Figure 19B).

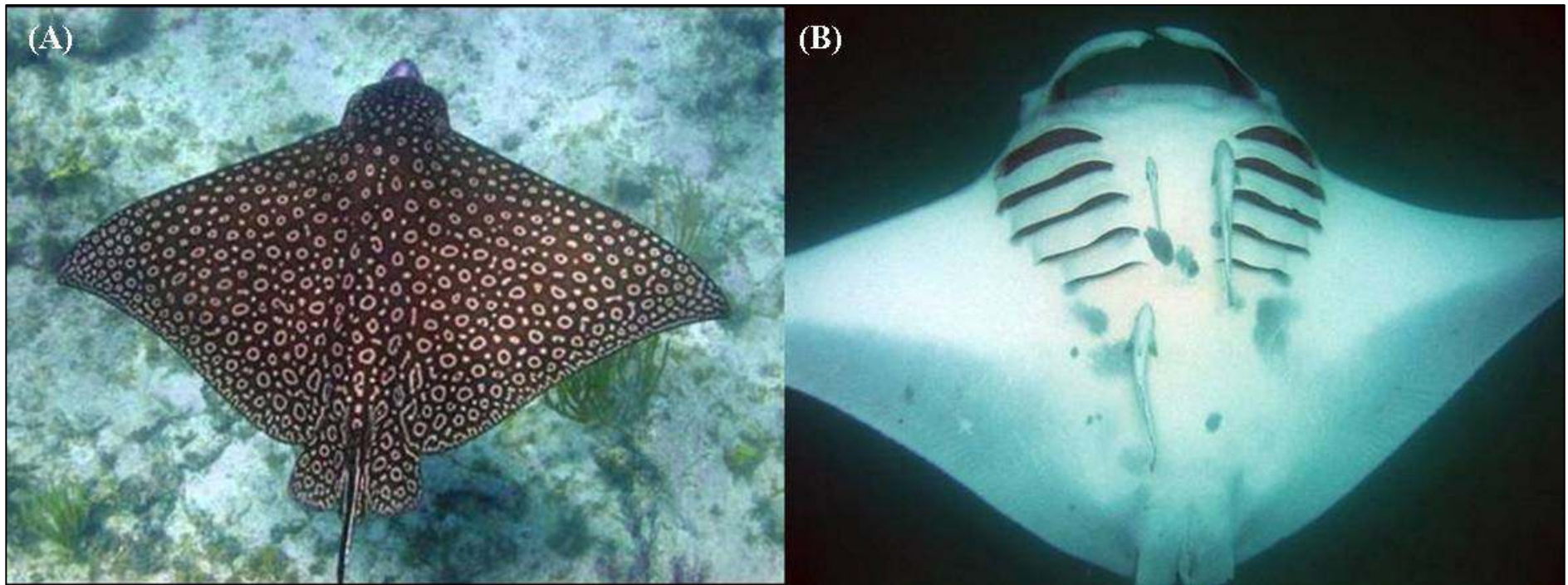


Figure 19. A) Spotted eagle ray (*Aetobatus narinari*) showing homogenous spot pattern on dorsal surface, B) Manta ray (*Manta birostris*) ventral surface with sparse, irregular spot pattern.

Species of teleosts such as the potato cod (*Epinephelus tukula*) may also be well suited to use with I³S due to their spot pattern and slow moving nature. Terrestrial species such as the spotted hyena (*Crocuta crocuta*), the spotted deer (*Axis axis*), and the spotted tail quoll (*Dasyurus maculatus*) could also be suitable. Additional organisms that are potential candidates include: felids, some cetaceans, many birds, amphibians and reptiles, and other elasmobranchs (Fig.1). While the potential application of I³S to animals with some form of spot pattern is broad, large, slow moving organisms with little flexion within the reference area are ideal.

I³S was particularly well suited to match spot patterns found on whale sharks because of their relatively stable spot pattern (Arzoumanian *et al.* 2005 and Meekan *et al.* 2006) established for the sub-adult and adult stages. These are the only life stages that whale sharks are regularly observed in at Ningaloo Reef and other known major aggregation around the world (Colman 1997). Therefore, this method is the most beneficial for this species as it allows capture-mark-recapture estimates to be calculated in a free, non-intrusive, reliable and effective manner. For other species that are accessible throughout all life stages and that demonstrate spot patterns that change between infancy and adult stages such as leopards (*Panthera pardus*) (Liu *et al.* 2006) or indeed leopard sharks (*Stegostoma fasciatum*) (Daley *et al.* 2002) (Fig.20), it may be difficult to use natural variation in spot patterns for capture-mark-recapture purposes across all life stages.



Figure 20. Juvenile and adult leopard sharks illustrating the difference in skin patterns between life stages.

Due to the small size of whale sharks at birth (0.58m) (Joung *et al.* 1996) compared to their maximum size at adult hood ($> 13\text{m}$)(Compagno 2001), it is likely that spot and stripe pattern change at least partially between early life and later stages, despite similarities reported for the patterning of juveniles and adults (Joung *et al.* 1996). This factor is unlikely to affect current demographic estimates based on capture-mark-recapture for this animal, as they are rarely photographed in infant life stages.

Recommendations

Only clear photographs, where subjects are on horizontal angles of less than 30° should be included in an I³S database. As demonstrated, it is likely that photos where subjects are on angles $> 30^\circ$ will not be matched or will receive low information criteria weights, which would necessitate manual visual validation of images. Manual validation is recommended for any matches that receive information criteria weights that are near the threshold. Likewise, the effect of roll of subjects to matching success using I³S should be assessed in future studies. The annotation of spots for fingerprinting will vary depending on what part of the torso of the shark is visible during the roll; therefore, roll may possibly affect the matching process and could be assessed in a similar fashion to the assessment of horizontal angle. However, video footage of individual sharks at varying angles of roll would be required, which could only be obtained by filming sharks using a method designed specifically for this experiment.

Even though the information criterion algorithm accounts for the number of spot pairs assessed to provide information criteria weights and evidence ratios, the immediate matching process using I³S may be affected by the number of spots annotated in the fingerprint. Based on fingerprints created for images in the I³S database, it is ideal to use between 25 and 30 spots per fingerprint for whale shark photos. Too many spots annotated (e.g., 40), and the image will be consistently ranked as a likely match, simply due to that fact that there will be more potential matching pairs.

The I³S software is still in its infancy, and future versions will endeavour to incorporate additional features that may assist in the matching process. The inclusion of an identifier such as scarring or sex may assist in the matching process (Van Tienhoven *et al.* 2007) and reduce the number of potential images to be searched. Van

Tienhoven *et al.* (2007) also indicated that they may change the future versions of the software to include both left side and right side images in a unified database, which would minimise the potential for double-counting individuals.

Although I concluded that using one good image of each individual in the database for matching purposes was ideal, Van Tienhoven *et al.* (2007) recommend including 3 good images of the same individual in the image library. This approach will increase the number of images of the same individual at varying orientations which improves the pattern-matching performance of I³S. The inclusion of many images of the same individual in a database however, could potentially be problematic from an information theoretic stand point, in that the extra images would increase the uncertainty of matches, unless matches were accompanied with an intensive manual search. Therefore, I recommend using only 1 good image per individual, to minimise matching uncertainty and ensure that the operating speed of I³S is maintained. To make the analysis process more efficient and get unbiased image matches, it would be ideal to integrate the information criterion algorithm into the I³S program. This would also allow anyone who uses I³S to obtain information criteria weights and evidence ratios without having a knowledge of programming themselves. Not only would integration make the procedure more accessible to a wider range of users, it would also help bolster collaboration between researchers, which is essential for building large datasets for demographic estimation. Collaboration is vital for long-lived, wide ranging species such as the whale shark, as obtaining data across a wide spatial and temporal scale helps to ensure that a representative sample of the population and associated processes is achieved.

Estimating population size

The first population estimates for the aggregation of whale sharks at Ningaloo Reef were based on a dataset of images collected between 1992 and 2004, from which 184 individuals were identified manually (Meekan *et al.* 2006). Data from 2005 and 2006 were included in my analysis, in which an additional 24 individuals were identified (a total of 208 individuals). The first population estimates were based on 159 individuals, where either images for both sides or the right side were present (i.e., left side-only images were discarded to remove the possibility of double-counting

individuals). There were a similar number of individuals (157) identified for population assessment in my study. Meekan *et al.* (2006) identified 33 individuals which were resighted between 1992 and 2004, which compared to 30 individuals identified by I³S in my study between 1992 and 2006. Despite the Meekan *et al.* (2006) study having fewer sampling occasions, fewer individuals were identifiable in my study due to a large number of images being incompatible for matching with I³S.

Population estimates based on data obtained via I³S matches were similar to the initial open population estimates found by Meekan *et al.* (2006) – the Ningaloo super-population (i.e. the population of individuals that visit Ningaloo Reef) is between 300 and 500 individuals based on open population models, with closed population estimates providing a much wider range (176-8696). This provides evidence to support hypothesis that initial population estimates made by eye were a reasonable approximation. The relatively high number (12 of 26) of known inter-annual resights that were not validated using information criteria weights was most likely due to oblique horizontal angles of subjects in images found in the I³S validation tests (Fig.18). The resights that had information criteria weights below the pre-determined certainty threshold (0.2) were removed from the capture matrix prior to population re-analysis to remove any uncertainty in resights. The information criteria weights and evidence ratios provide a measure of match parsimony based on the strength of matches, which can be misleading if the quality of images compared are poor (see Friday *et al.* 2000). Therefore, rather than dismissing resights completely based on low information criteria weights or evidence ratios, it is more appropriate to make the final decision by manual inspection under these circumstances.

The use of validated images for population estimation has provided a measure of certainty in resights and resultant estimates of population parameters such as abundance and vital rates (e.g., survival and population trajectories; Bradshaw *et al.* 2007). The validation of image matches also assists in reducing identification errors which are common in photo-identification, such as false-positives and false-negatives. These types of errors can greatly inflate population estimates (Stevick *et al.* 2001), which can have serious implications for the management of threatened populations. Population estimates for whale sharks at Ningaloo Reef are based on the assumption

that their spot and stripe patterns remain stable through time. Therefore, if ontogenetic changes in spot patterns do occur, the number of individuals resighted will likely be underestimated and estimates of population size would be upwardly biased (Meekan *et al.* 2006).

In addition to data quality, sampling effort has the potential to affect estimates if it has varied over sampling periods. Sampling effort varied between the periods of 1992-2003 and 2004-2006 in this study. This variation in sampling effort may be a contributing factor to the few resights seen in recent years; nevertheless, population estimates should be viewed tentatively until enough image matches are obtained to reduce uncertainty (Meekan *et al.* 2006). Future estimates of population size should be facilitated by a recent policy of photo sharing implemented by the Western Australian Department of Environment and Conservation (DEC) which states that all photos taken of whale sharks by tour operators and research vessels in Ningaloo Marine Park must be pooled at the end of the season. This will assist in standardising sampling effort, and will also ensure that a representative sample of the whale shark population visiting Ningaloo each season is obtained.

Conclusion

The validation technique I have developed provides a relatively non-subjective method of assessing the quality of image matches obtained through photo-identification studies. The validation of whale shark image matches made by I³S using an information criteria algorithm provided a threshold of 0.2 for information criteria weights, below which obtaining a successful match was unlikely. This threshold may vary between organisms; however 0.2 is a conservative and recommended starting point. Matching performance of I³S decreased considerably as the horizontal angle of subjects in images increased. Known matches were matched successfully for images where subjects were on horizontal angles of up to 30°. It was determined that the number of matching spot pairs may also have an effect on matching success. By incorporating for the number of matching spot pairs into the information criterion algorithm, information criteria weights and evidence ratios that are impervious to the number of matching spot pairs were achieved. In addition to angle, the affects of ‘roll’ of subjects in images likely has an affect on the matching process, and should be investigated in future studies. The use of I³S (freely

downloadable from www.reijns.com/i3s) in conjunction with the information criterion algorithm is recommended for reliable photo-identification of animals with stable spot patterns.

The analyses of whale shark population estimates for both non-validated and validated resights yielded similar results that were analogous to estimates obtained by Meekan *et al.* (2006), where images were matched by eye. Open population estimates provided the most likely scenario with super-population estimates falling between 250 and 500 individuals. Despite the validation of resights, abundance estimates should be viewed with care due to low numbers of individuals resighted in recent years.

Due to the simplicity and accessibility of I³S and the validation technique, collaboration between researchers is encouraged, which can potentially assist in building a more accurate knowledge base of populations being monitored. Rapid, reliable and non-intrusive population monitoring is vital for wild animals which are threatened by environmental and anthropogenic factors. It is hoped that the technique presented in this study will assist in the conservation of whale sharks through population monitoring, and will also hold great promise for other populations of animals similarly threatened with extinction. Reliable, effective photo-identification and demographic estimation for animals with stable, natural markings is now possible for anyone armed with a digital camera.

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APPENDIX 1. Text output from an I³S search

Image Name	Spot Pairs Matched	I ³ S Score
NIN.01041993.M.R.PRN.GT.3c.jpg	26	0.0
NIN.13041992.M.R.PRN.GT.2g.jpg	25	0.026697512223308146
NIN.12041995.M.R.PRN.GT.2b.jpg	20	0.17498936942429538
NIN.31031993.M.R.PRN.GT.1a.jpg	18	0.19136027670168385
NIN.06041994.M.R.PRN.GT.1e.jpg	19	0.1994483117636937
NIN.12041996.M.R.PRN.GT.2a.jpg	19	0.19956653140667022
NIN.03041994.M.R.PRN.GT.2a.jpg	16	0.19959835491728176
IMG341.jpg	20	0.19971634314588813
NIN.05052004.F.R.VID.CM.2b.jpg	19	0.2097406387782817
IMG337.jpg	18	0.21667996704635697
NIN.01041993.M.R.PRN.GT.1d.jpg	19	0.22499807394611407
NIN.24052003.U.R.VID.SQ.2a.jpg	17	0.22860006159925247
NIN.02041995.R.PRN.GT.1a.jpg	18	0.234701403008934
NIN.22052003.U.R.VID.SQ.2a.jpg	15	0.23734399107451162
NIN.05041994.U.R.PRN.GT.2d.jpg	17	0.2399006790999126
NIN.07041993.M.R.PRN.GT.1a.jpg	17	0.24089443788524306
NIN.13041992.U.R.PRN.GT.2c.jpg	18	0.24592754083740107
IMG0030.jpg	16	0.24659260972041333
NIN.04052003.U.R.VID.SQ.2a.jpg	18	0.2483985645538132
NIN.21052003.U.R.VID.SQ.2a.jpg	18	0.2520428408503968
IMG323.jpg	19	0.2525053217048749
NIN.15052003.U.R.VID.SQ.1a.jpg	17	0.2527715075730004
NIN.05041994.M.R.PRN.GT.1a.jpg	15	0.2554023662542289
NIN.09041995.F.R.PRN.GT.2a.jpg	19	0.2662161295197267
NIN.06041994.F.R.PRN.GT.2a.jpg	18	0.2664327778448554
NIN.03041994.M.R.PRN.GT.2b.jpg	18	0.2670534005173172
NIN.03041994.M.R.PRN.GT.2d.jpg	19	0.2690595886195092
NIN.06041996.M.R.PRN.GT.2a.jpg	16	0.27114544833122617
NIN.17052004.M.R.VID.AR.2a.jpg	16	0.271926268628287
NIN.05072001.U.R.VID.SQ.2a.jpg	17	0.27343986754945016
NIN.08062001.U.R.VID.SQ.3d.jpg	16	0.27734400181939595
NIN.31031993.M.R.PRN.GT.2c.jpg	15	0.2809263157076504
NIN.13041992.M.R.PRN.GT.1f.jpg	17	0.28132617119010783
NIN.03041996.M.R.PRN.GT.2d.jpg	18	0.28155600721497015
NIN.09052001.U.R.VID.SQ.2a.jpg	17	0.2820968823438963
NIN.05041996.M.R.PRN.GT.1d.jpg	17	0.2849783546636983
NIN.02041996.F.R.PRN.GT.2c.jpg	15	0.28683605073347856
IMG278.jpg	19	0.29003726559013765
NIN.03041996.M.R.PRN.GT.2c.jpg	18	0.29390018972048787
NIN.05041996.F.R.PRN.GT.2c.jpg	18	0.29756122470813395
NIN.11052001.U.R.VID.SQ.3a.jpg	18	0.30113817405806126
NIN.15052001.U.R.VID.SQ.1a.jpg	19	0.30794794468421455
NIN.18041992.U.F.R.PRN.GT.3a.jpg	16	0.31253349265575037
NIN.14041992.M.R.PRN.GT.2c.jpg	17	0.3168102183877455
NIN.09052003.U.R.VID.SQ.3a.jpg	14	0.32731837191972896
NIN.13041994.F.R.PRN.GT.2c.jpg	17	0.32800933326863635
NIN.02041996.M.R.PRN.GT.2b.jpg	15	0.3313375771375459
NIN.04072001.U.R.VID.SQ.1a.jpg	16	0.33868355513512527
NIN.31031996.M.R.PRN.GT.2b.jpg	15	0.3402600444316305
IMG339.jpg	14	0.3483577459761844

***Note. The first image in the list was present in the database already; therefore it was matched with itself, and resulted in an I³S score of 0. The second image in the list is therefore the most likely match. Text outputs such as this were used to import data into the statistical program R.**

APPENDIX 2. R code for information criterion algorithm

```
#####  
## R code (R Code Development Team 2004 - www.r-project.org)  
## to calculate Information Criterion (IC) weights from text  
## outputs derived from Interactive Individual Identification  
## Software (I3S), formerly known as 'Individual Raggie  
## Identification ## System (IRIS)  
#####  
  
#####  
## Code developed by CJA Bradshaw & CW Speed ©  
## Charles Darwin Universtiy, Darwin, Australia  
## Email: corey.bradshaw@cdu.edu.au  
## September 2006  
#####  
  
#####  
## This code accompanies the manuscript entitled:  
## Spot the match – wildlife photo-identification using information theory  
## by CW Speed, MG Meekan, CJA Bradshaw  
## Frontiers in Zoology  
#####  
  
## Establish target folder containing I3S text outputs (e.g.)  
folder <- "C:"  
  
## Establish I3S text output of scores  
file <- "file.name"  
  
## Calculate Information Criteria and weights  
target.file <- paste(folder,file,sep="")  
  
## Import data  
dat <- read.table(target.file,header=F)  
colnames(dat) <- c("image","spots","score")  
  
## Information Criterion  
IC <- 2+((100*(1/dat$spots))*log((dat$score*dat$spots^2)/(100*(1/dat$spots))))  
IC <- IC[-1]  
  
## delta IC  
dIC <- IC - min(IC)  
  
## IC weight  
wIC <- (exp(-0.5*dIC))/sum(exp(-0.5*dIC))  
  
## Best matching image IC weight  
best.ICw <- wIC[1]  
  
## Best matching image information-theoretic evidence ratio (ER)  
best.ER <- wIC[1]/wIC[2]
```

APPENDIX 3. Spot the match – wildlife photo-identification using information theory (manuscript)