Abundance of east coast Australian humpback whales (*Megaptera novaeangliae*) in 2005 estimated using multi-point sampling and capture-recapture analysis.

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ABSTRACT

The humpback whales (*Megaptera novaeangliae*) that migrate along the east coast of Australia were hunted to near extinction during the last century. This remnant population is part of Breeding Stock E. Previous abundance estimates for the east Australian portion of Breeding Stock E have been based mainly on land-based counts. Here we present a capture-recapture abundance estimate for this population using photo-identification data. These data were collected at three locations on the migration route (Byron Bay – northern migration, Hervey Bay and Ballina - southern migration) in order to estimate the population of humpback whales that migrated along the east coast of Australia in 2005. The capture-recapture data were analysed using a variety of closed population models with a model-averaged estimate of 7041 (4075 – 10008 95% C.I.) whales.

Key Words: humpback whale, breeding stock E, abundance estimate, photo-identification, capture-recapture.

INTRODUCTION

Humpback whales *Megaptera novaeangliae* in the Southern Hemisphere undertake an annual migration during the austral winter months from their Antarctic feeding areas in higher latitudes to their tropical breeding areas (Chittleborough 1965; Paterson 1991). There is temporal segregation of different classes of whales on this migration, with lactating females and yearlings the first to leave the feeding grounds, followed by immature whales of both sexes, mature males and resting females, and lastly pregnant females migrating to the breeding grounds (Dawbin 1966, 1997). On the return journey to the Antarctic feeding grounds, newly pregnant females are the first to leave tropical waters, followed by immature whales, mature males and resting females, and lastly mothers with calves (Dawbin 1966, 1997). Chittleborough (1965) concluded that the population of humpback whales that migrate along the east coast of Australia comprises part of the Area V population (130^0 0' E to 170^0 0' W). This population was previously known as Group V. Recent studies suggest that the region contains several populations that intermingle to a variable but probably small degree (Garrigue *et al*., 2000, 2007). Group V humpback whales have now been divided into three sub-stocks known as Breeding Stock E(i), those wintering off the Australian east coast, E(ii), those wintering around New Caledonia, and E(iii), those wintering around Tonga (IWC, 2005; Olavarria *et al*. 2006). Breeding Stock E(i), the Australian east coast population, is thought to be the largest of these.

Last century, the Area V humpback whale population was subjected to both land and vessel-based hunting from a number of locations throughout its migratory range, including the east Australian coastline and

Antarctica. Prior to the 1950s there was little exploitation of this east Australian population. At this time the population size of the entire Group V population was estimated to be between 10,000 and 26,000 whales (Chittleborough 1965; Bannister and Hedley 2001). However, these figures are potentially an underestimate of the pre-exploitation population for Group V. The total number of 20th century and post World War II humpback whale catches in Area V and their purported breeding area (E) was 64,252 (Clapham and Zerbini 2006) and 38,146 respectively (Clapham *et al.,* 2005). Therefore, it can be assumed that the pre-exploitation population was likely to have been larger for Group V, potentially in the range of 30,000 to 40,000 humpback whales (Jackson *et al*., 2006).

Massive illegal pelagic whaling in the Southern Ocean, coupled with industrial shore-based whaling, resulted in a major population collapse by 1962 (Chittleborough 1965; Clapham *et al*. 2005). Estimates of the remaining population varied from 104 for all of Group V (Bannister and Hedley 2001) to 500 for the east Australian and New Zealand populations (Chittleborough 1965), which represents less than 5% of the original estimated population.

Since 1963, the east Australian population of humpback whales has shown signs of partial recovery (Paterson *et al*. 2001; Brown *et al*. 2003; Noad *et al.* 2005). The apparent lack of recovery of the humpback whale population migrating past New Zealand (Gibbs and Childerhouse 2004, Constantine *et al*. 2007), and low numbers recorded in some regions of the South Pacific (Garrigue *et al*. 2000, 2002), suggest that most of the humpback whales remaining in Area V at the termination of whaling probably form the east Australian population. The most recent abundance estimate for the east coast Australian population of humpback whales utilised land-based counts at Stradbroke Island, Queensland, with an estimate for the 2004 season of 7090 ±660 (95%C.I.) (Noad *et al.* 2005). However, all methods of estimating abundance have inherent assumptions and biases. Therefore, a more robust population estimate can be obtained by using a number of techniques.

The technique of identifying individual humpback whales by photographing the underside of their tail flukes is widely accepted (Katona *et al*. 1979; IWC 1990), and has been used extensively for capture-recapture analyses to estimate population parameters and abundance (e.g. Hammond 1986, Buckland 1990, Calambokidis *et al*. 1990, Smith *et al.* 1999, Urban *et al*. 1999, Calambokidis and Barlow 2004).

This study represents a capture-recapture population estimate for the portion of the humpback whale Breeding Stock E, which migrated along the east coast of Australia during 2005, using multipoint sampling and fluke identification photographs. To date, most of the estimates of the abundance of the eastern Australian humpback whale migration have been based on simple counts and distance sampling methods. This population estimate is based on an analysis of an ongoing data set of photo-identification data collected by the authors. We have used the 2005 photo-identification data to establish a point of reference for future photo-identification studies and to provide a point comparison of estimates obtained independently by distance sampling and capture-recapture methods.

METHODS

Study Areas and Survey Effort

Three sampling sites were used on the humpback whale migratory corridor on the east coast of the Australian mainland: Byron Bay in northern New South Wales (NSW), Hervey Bay in Queensland (Qld), and Ballina in northern NSW. All three sites are the locations for long-term independent studies by four of the authors (DP, DB, TF, WF) on the biology, behaviour and population characteristics of eastern Australian humpback whales.

Vessel based photo-identification surveys were undertaken as whales migrated past each of the study sites within one migratory season during the 2005 austral winter and spring months (June – November 2005). Field surveys at each of the study sites were timed to include the major part of the migration on either side of the peak past that location (Paterson 1991; Dawbin 1997). Due to the timing of the migration and the locations of the three study sites on the migration corridor, surveys commenced first at Byron Bay during the northern migration, followed by surveys in Hervey Bay and Ballina on the southern migration. There was limited temporal overlap (6 days) between sampling during the northern migration at Byron Bay and the commencement of sampling in Hervey Bay during the southern migration. Surveys at Hervey Bay and Ballina were undertaken mostly concurrently during the southern migration. Geographical location, survey effort and equipment used are summarised in Table 1.

The study sites of Byron Bay and Ballina are on the migratory corridor at, or close to, the most easterly point of the Australian mainland, where the vast majority of humpback whales migrate within 10km of the coast (Bryden 1985). The width of the humpback whale migration corridor was re-assessed in 1991 (Brown 1996) and 2007 (Noad and Dunlop 2007), and found to be consistent with the results of Bryden (1985). Humpbacks travel past Ballina and around the eastern point of Australia at Byron Bay, in both a northerly and southerly direction, en-route between the Antarctic feeding grounds and the Great Barrier Reef breeding grounds (Paterson 1991). At Byron Bay and Ballina, the research vessel was assisted in finding pods of whales by a team of land-based observers using the "Cyclopes" (theodolite/computer) whale tracking system (Kniest and Paton 2001).

The third study site is located in Hervey Bay, a sheltered, shallow bay formed between the Queensland coast and Fraser Island, 60 nautical miles below the southern end of the Great Barrier Reef. During the southern migration, many humpback whales travel into and out of the eastern side of Hervey Bay from the north. The distance between Hervey Bay and the Byron Bay and Ballina study area is approximately 550km (Figure 1).

A standard sampling protocol for photo-identification was adopted for each sampling site. Photography of ventral fluke surfaces was obtained during a maximum of ten terminal dives and/or a maximum of 45 minutes with each pod (Smith *et al.* 1999). Photographs of the ventral fluke surface of calves were not included in this study. All images were cropped to a common 3 x 2 pixel ratio as high quality jpeg digital files.

Photo-identification analysis

The principal photographers examined all images for each of their respective study sites and selected the best single photograph for each individual whale. Composites of multiple images of a single fluke were constructed if these provided sufficient information to accurately identify the whale (see Figure 2). All images for each study site were assessed for within-season resights to eliminate duplicates.

In order to produce the final dataset for analysis, the principal photographers then collectively reviewed the fluke catalogue for each sampling site using a protocol developed in the northern hemisphere for grading humpback whale fluke identification photograph quality (Calambokidis *et al*. 2001). This included scoring all flukes according to five different characteristics of photo quality: (1) exposure / contrast / lighting; (2) fluke angle; (3) photographer / lateral angle; (4) focus / sharpness; and (5) proportion of fluke visible. Each photograph was given a score from 1 to 5 (highest quality to lowest) for each characteristic, and all flukes with at least one score of 4 or lower (5) were excluded from the dataset.

Prior to matching, each of the principal photographers stratified their catalogue according to one of two independently-evolved fluke matching systems: the Byron Bay and Ballina fluke catalogues were stratified using a system developed by one of the authors (DB), while the Hervey Bay catalogue was stratified using a system developed by another author (TF). The stratified matching systems used in this analysis are based on individual fluke characteristics including percentage black, characteristics of the centre and characteristics of the trailing edge of the fluke for each identification photograph. These systems were used to reduce the number of comparisons required in the matching process.

Pair matching using digital images was conducted by two independent matchers for each site as follows: DB matched Ballina against the Byron Bay and Hervey Bay Catalogues, DP matched Byron Bay against the Ballina and Hervey Bay Catalogues, and TF matched Hervey Bay against the Byron Bay and Ballina Catalogues. All matched flukes, including matches found by only one of the two matchers, were collectively reviewed and reconciled.

Statistical models

Our approach to estimation assumed that the population was closed to immigration, emigration, births and deaths during the sampling period and that images of the same individuals were reliably matched (i.e., no tag loss). After assessing the credibility of the closure assumption and the likelihood of tag loss, we considered a number of different assumptions about the sources of variation in capture and recapture probabilities that might be incorporated in models; whether capture probabilities varied by occasion (temporal variation), differed on any occasion between previously captured and newly captured individuals (behavioural response) or varied among individuals (heterogeneity). The program CAPTURE (Otis *et al*., 1978; Rexstad and Burnham, 1991) was employed to provide an initial indication of the most likely sources of variation. Finally, the program MARK (Version 5.0: www.phidot.org/software/mark/) was employed to fit and compare a set of credible models.

Population closure

The data were collected within one migratory cycle (within a 6 month period). It is assumed that whales migrating north past Byron Bay during the northern migration of 2005 returned south to the feeding grounds along the east coast of Australia during the southern migration and were potentially available for capture at Hervey Bay and/or Ballina. This assumption is supported by a study of genetic diversity (Olavarria *et al.* 2006), an analysis of interchange rates between eastern Australia and Oceania based on photo identification (Garrigue *et al*., 2007) and within-season returns of Discovery marks in the region (Dawbin 1964). Deaths, immigration, and emigration were assumed to have had negligible effects on the estimate. Calves were not included in this analysis, thereby eliminating the effects of births or calf mortality. Therefore, for the purposes of this analysis, the population was considered to be closed.

Tag loss

Effective tag loss resulting in an overestimate of the population size may have occurred in this study if flukes changed markings between sampling occasions, and might have occurred if poor quality, difficult-to-match photographs had been included. Significant changes in natural fluke markings are likely to have been minimal during the short survey period. The use of a widely accepted protocol, based on photo quality (*Calambokidis et al.* 2001), minimises the potential for tag loss due to poor image quality.

A further source of effective tag loss may be human error in failing to match fluke photographs. By using two independently evolved stratification systems and having two independent matchers each separately conduct the match for each site, before reconciling the results, the probability of missing a match is considered to be low.

Time-specific capture probabilities

Survey effort varied among the sites (Table 1) with approximately 397, 440 and 255 survey hours at Byron Bay, Hervey Bay and Ballina respectively. Environmental conditions, vessel speeds and survey protocols also varied slightly. It is highly likely therefore that capture probabilities were variable among the sites and lower at Ballina than at the other two sites in particular.

Behavioural response

Whilst there is no reason to expect that whales either sought or avoided the survey vessels following capture, there is reason to consider it possible that apparent behavioural response was present in the data due to non-random mixing between samples. Dawbin (1966, 1967) reported that the migration is structured in a temporal sequence led by lactating females and yearlings, immature whales of both sexes, mature males and resting females, and lastly pregnant females migrating to the breeding grounds. This sequence is largely the same during the migration south, with newly pregnant females the first to leave the breeding grounds, followed by immature whales, mature males and resting females, and lastly mothers with calves (Dawbin 1966, 1997). Although the surveys were timed to spread across a sizeable part and centred on the expected peak of the migration past each of the sites, it is possible that such classes of whales were not present in the same proportions during the survey periods at the three sites. Under these circumstances, the whales captured at a site may be more or less prevalent with probabilities of recapture at subsequent sites that differ from the probabilities of first capture at those sites, inducing apparent behavioural response.

Heterogeneity of capture probabilities

The probability of capture of a whale is conditional on the time it is available for capture at a site, its response to vessels and its fluking behaviour. The typical time spent in the presence of vessels and the typical frequency and duration of fluking activity may vary among such classes of whales as immature whales, mature resting females, mature males and mothers with calves (Rice *et al.* 1987). Following the previous example, mothers with calves may be more or less likely to fluke up than other whales and indeed may typically spend a shorter or longer period in Hervey Bay. Therefore, heterogeneity of capture probabilities is possible.

Tests of assumptions and goodness of fit
The seven tests from program CAPTURE (Otis *et al*., 1978; Rexstad and Burnham, 1991) were run to gain insight into a likely appropriate model structure. However, given the potential complexity of the data-generating process and a high probability of time-specific capture probabilities, it's notable that CAPTURE provides no tests for the pertinent comparisons of M_t vs. M_{th} or M_t vs. M_{tb}.

The full likelihood-based closed capture models available in the program MARK (Version 5.0: www.phidot.org/software/mark/) provide a means of fitting a number of models of the forms M_t and M_{tb} (Otis *et al*., 1978). These models were compared by means of the minimum AICc criterion (Williams *et al*., 2001), and estimates from a set of selected models were averaged following the procedure of Buckland *et al*. (1997). We restricted our modelling to these models except for the non-likelihood based M_{th} model of Chao *et al*. (1992) which was employed to provide an informal comparison of its estimate to those from the M_t and M_{tb} models referred to above.

RESULTS

A total of 1085 fluke photographs were assessed for inclusion in the analysis (Byron Bay 406, Hervey Bay 391, Ballina 288). Following collective evaluation of each image against the photograph quality protocols, 222 fluke photographs were excluded from the dataset based on photographic quality. The final dataset comprised a total of 863 fluke photographs (Byron Bay 343, Hervey Bay 321, Ballina 199). Of these, 829 whales were determined to be unique individuals, with a total of 34 (4.1%) whales being captured at two different survey sites during the study period. No whales were sampled at all three survey sites within the study period. The matches and frequencies of capture histories are reported in Table 2.

Tests of the assumptions
The goodness of fit tests from program CAPTURE (Otis *et al*., 1978; Rexstad and Burnham, 1991) indicated probable behavioural response (test 2: M_0 vs. M_b), probable time-specific variation in capture probabilities (test 3: M_0 vs. M_t), probable heterogeneity in capture probabilities (test 4: M_h vs. not M_h), probable behavioural response (test 5: M_b vs. not M_b), and probable behavioural response in the presence of heterogeneity (test 7: M_h vs. M_{bh}). The expected values were too small to test for heterogeneity (test 1: M_0 vs. M_h) or time-specific variation (test 6: M_t vs. not M_t). CAPTURE suggested that the appropriate model was probably M_{tb} but encountered a computational problem in trying to fit the model and did not produce a reliable estimate (offering 28581).

Among the set of eight full and reduced M_t and M_{tb} likelihood based models (Otis *et al*., 1978) that might notionally be fitted, it was not possible to simultaneously estimate the six parameters of the most general of these models with different capture probabilities at each site and recapture probabilities different both to each other and any capture probability. This is because at least one constraint relating the capture and recapture probabilities is required for identification. Among the remaining seven models of this type, a model that proposed equal capture probabilities in Byron Bay and Hervey Bay and that the two recapture probabilities differed both from each other and from any capture probability also lacked the required constraint and produced an unrealistically low estimate of population size (3059). Pertinent results from the remaining six models are reported in ascending order of AICc in Table 3.

Among a small set of models that assumed equal capture probabilities, the best fitting (111234) had an AICc that was 5.59 larger than the worst fitting of the M_t and M_{tb} models in Table 3 (123245) indicating, as expected, a high probability of time-specific variation in capture probabilities.

For comparison with the estimates provided by this set of models, the M_{th} model (Chao, et al., 1992) from program CAPTURE provided an estimate of 7014 (5163 - 9685, 95% C.I.) with equal probabilities of capture off Byron Bay and in Hervey Bay.

Model selection

The deviances of these models were very similar and the minimum AICc criterion accordingly ordered the models largely in terms of parsimony: i.e. it favoured models with fewer parameters. Although c-hat could not be estimated, an experiment in which its value was assumed to be 2 resulted in the more parsimonious models being even more strongly favoured in terms of relative AICc values.

Population estimate

The range of population estimates (6303 – 7843) among the models reported in Table 3 was not wide relative to the width of the confidence intervals. Consequently, the considerable uncertainty encountered in selecting among the models on the basis of AICc was not as serious a limitation on obtaining a reasonable estimate as it might otherwise have been. However, if only one of these models were to be chosen for interpretation it would be the simplest, with a likelihood nearly twice the size of that of the next most likely model: i.e., the 3-parameter model (112123) which assumed equal capture probabilities at Byron Bay and in Hervey Bay, and recapture probabilities equal to capture probabilities (no behavioural response). Further in favour of this model, if overdispersion were present in the data, as would be reflected in a higher c-hat, its likelihood would have been even greater relative to the other models. This model provided an estimate of 7024 (5163 - 9685, 95% C.I.) whales, which lies approximately in the middle of the range of the several estimates. Nonetheless, while apparent behavioural response cannot be excluded theoretically, and the four models in the set that do assume some form of apparent behavioural response cannot be reliably distinguished among nor from the simpler models by the AICc criterion, it may be appropriate to use the very similar model-averaged estimate of 7041 (4075 - 10007, 95% C.I.) whales.

None of the models considered so far has treated animal level heterogeneity of capture probabilities. As a point of reference, the M_{th} model of Chao *et al.* (1992) provided an estimated population size of 7014 (5133 - 9718, 95% C.I.) whales.

DISCUSSION

This collaborative study represents a multi-point sampling capture-recapture abundance estimate using photo-identification for humpback whales migrating along the east coast of Australia during 2005. It was known from previous research that the migration has a temporal sequence of different classes of whales. It was considered particularly important on this account that the surveys at each site were timed to include the major part of the migration on either side of the peak past that location in order to repeatedly sample from the entire population rather than from a somewhat different subset at each site. We expected that apparent behavioural response would be manifested in the models to the extent that we were unsuccessful in this and that the whales sampled at one site were present in greater or lesser proportion at another. There was some evidence of this in as far as the models displaying a behavioural response structure could not be reliably distinguished from those that didn't by the AICc criterion. Nonetheless, the simplest model with equal capture probabilities at Byron and Hervey Bay and no behavioural response had twice the likelihood of any behavioural response model. While this situation may have created a dilemma had these models produced markedly different population estimates, the similarity of the estimate from this model and the model averaged estimate which included the behavioural response models is reassuring.

Another recent abundance estimate for this population was based on land-based counts from Stradbroke Island, with an estimate for the 2004 season of 7090 ± 660 (95% C.I.) and an annual increase of 10.6± 0.5% (95% C.I.) (Noad *et al*. 2006). Extrapolating this figure to 2005 would produce an estimate of 7842 (7112 – 8572, 95% C.I.). Here we have estimated of the number of whales that migrated along the east coast in 2005 and provide a single best estimate of 7024 (5163 - 9685 95% C.I.) whales and a model averaged estimate of 7041 (4075 - 10007 95% C.I.) whales.

Further considerations

Data collection over a series of seasons would enable a more accurate, reliable and informative analysis through the use of a robust design model (e.g., Kendall *et al*., 1995, 1997; Kendall and Nichols, 1995).

This analysis only considers humpback whales that undertook migration along the east coast of Australia during 2005. However, Brown *et al*. (1995) suggested that a percentage of females may not undertake the migration annually. This hypothesis could be tested by undertaking inter-year capture-recapture studies.

Chaloupka *et al*., (1999) suggest that only a portion of the whales migrating along the east coast of Australia enter Hervey Bay and therefore would not be available for sampling in Hervey Bay. This factor will not bias this analysis assuming that these whales were available for capture at Byron Bay and Ballina. Aerial surveys off the coast of Byron Bay and Ballina would also help to establish the width of the current migration corridor, and determine whether it is possible that some whales are not available for capture at any of the three sites because they migrate further offshore at Byron Bay and Ballina and don't enter Hervey Bay.

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Table 1: Summary of Locations, survey effort and equipment utilised.

	Byron Bay	**Hervey Bay**	**Ballina**
Migration direction	North	South	South
Latitude / Longitude	28^{0} 37’ S, 153^{0} 38’ E	25^{0} 00’ S, 153^{0} 00’ E	28^{0} 52’ S, 153^{0} 37’ E
General geography	Open ocean off most easterly point of Australian mainland	Shallow, sheltered bay close to western shore of Fraser Island	Open ocean off Ballina and Lennox Head
Dates of survey	4-6-05 to 12-8-05	7-8-05 to 14-10-05	17-8-05 to 04-11-05
Survey Period	69	68	79
Number of Survey Days	50	60	39
Daily effort (Av hours per day)	7hrs 56mins	7hrs 20mins	6hrs 32mins
Research vessel	5.4-metre centre console powerboat	12-metre power catamaran	5.8-metre centre console powerboat
Photographic equipment	Canon EOS 20D, 100-400mm lens F3.5 –5.6 L IS	Canon EOS 20D, 100-300mm lens F3.5-5.6	Nikon D100, 70-200mm lens F2.8 VR, and 1.4X converter
Supported by land-based spotters	Yes	No	Yes
Principal photographer	DP	TF	DB

Table 2 Frequencies of capture histories

Byron Bay	Hervey Bay	Ballina	Frequency
1	0	0	319
0	1	0	297
0	0	1	179
1	1	0	14
1	0	1	10
0	1	1	10
1	1	1	0

Table 3 Results from six full and reduced Mt and Mtb models

Model[1]	AICc	ΔAICc	AICc wt.	Likelihood	Params.	Deviance	Nhat	SE	L95%CI	U95%CI
112123	-7417.436	0.000	0.340	1.000	3	10.462	7024	1139	5163	9685
123234[2]	-7416.195	1.241	0.183	0.538	4	9.697	7021	1138	5160	9680
112324	-7416.033	1.403	0.169	0.496	4	9.859	6303	1298	4290	9486
112134	-7415.775	1.662	0.148	0.436	4	10.118	7843	2007	4876	12985
123435	-7414.554	2.883	0.081	0.237	5	9.330	6447	1346	4365	9754
123245	-7414.528	2.908	0.079	0.234	5	9.356	7834	2005	4871	12971

1. The models are numbered according to their parameters: capture probabilities in Byron Bay, Hervey Bay and Ballina, recapture probabilities in Hervey Bay and Ballina, and the estimated population size. Where a subsequent parameter is specified as equal to a previous one, the previous parameter number is used. For example, model 112123 indicates the same capture probabilities in Byron Bay (1) as in Hervey Bay (1) but a different capture probability off Ballina (2); that the recapture probability in Hervey Bay is the same as the capture probability in Hervey Bay (=Byron Bay) (1) , and that the recapture probability off Ballina (2) is the same as the capture probability off Ballina (2). The population estimate parameter takes the next value (3).

2. Darroch M_t

Figure 1: Study Area

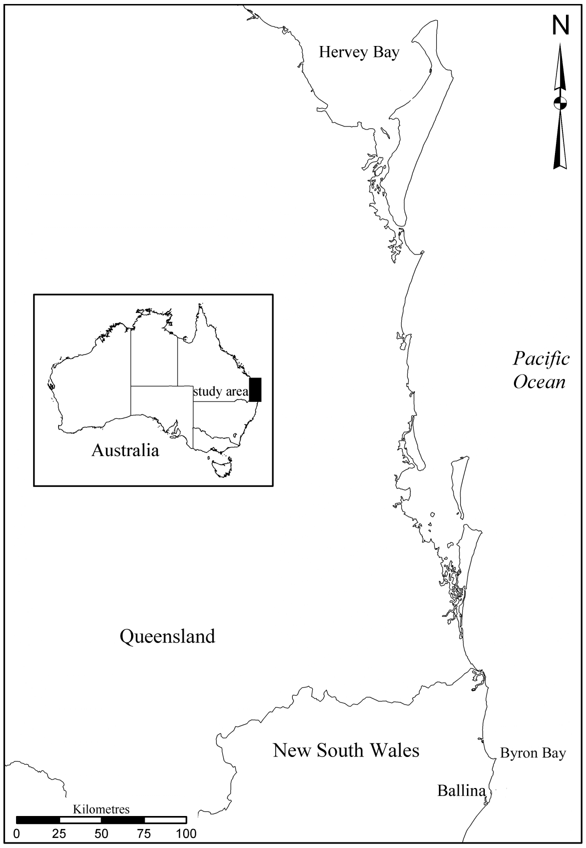

Figure 2. Example of a composite image used in the analysis.