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Daily net emigration from a spawning concentration of chokka squid (*Loligo vulgaris reynaudii* d'Orbigny, 1845) in Kromme Bay, South Africa

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The net emigration from a spawning concentration of the loliginid squid, *Loligo vulgaris reynaudii* d'Orbigny, 1845, was investigated quantitatively using a combination of tagging and hydroacoustic techniques, midwater trawling, purse seining and SCUBA diving. Aquarium experiments were used to supply additional information on tag loss and mortality from tagging. The number of squid in a concentration containing T tagged individuals was assessed hydroacoustically and then c squid were caught by means of a midwater trawl or purse seine. It was assumed that the t_n tagged squids in these catches were the result of natural mortality, tagging mortality and net stability of the concentration (the result of emigration and immigration) n days after tagging. The average net emigration was then calculated to be 0.2 per day for 7.5 days of observations. This result is a first attempt to solve the so-called ''Hilborn's problem'', i.e. the problem of how to measure the aggregation dynamics of nektonic organisms in the sea (instead of modelling).

Key words: squids, hydroacoustics, tagging, migrations.

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Introduction

Marking of fish for research purposes is a widely used practice with a very old conceptual background (Ricker, 1975, p. 75). The objectives of such research are usually calculation of the exploitation rate, stock assessment (i.e. estimating the size of the exploited population (Ricker, 1975, pp. 75–148)) and/or understanding migration patterns (Harden Jones, 1970, pp. 18–24). The same general aims and principles may be applied to squid. Although squid may not be functionally comparable with fish (Packard, 1972 vs. O'Dor *et al.*, 1990), they have been described as ecologically similar (Longhurst and Pauly, 1987, pp. 322–334). Consequences of the short life cycle of squid are that only one mark-recapture model is viable, viz. the Petersen census (Ricker, 1975) and that most of what has been studied (e.g. Nagasawa *et al.*, 1993) relates to migration patterns.

Fish marking was initially developed in small ponds and lakes, where assumptions of the models developed may have been more easily tested (Ricker, 1975, p. 75). Most fish and all squid, however, live in the oceans, where such testing is very difficult or impossible and assumptions made are mostly left unchallenged. These are highlighted by Hilborn (1991), who points out that the models do not allow for mortality or emigration and that there is confounding between mortality of tagged fish, tag loss, tagging mortality, and reduced probability of capture of tagged fish. These problems, in the opinion of Nagasawa *et al.* (1993) should also be addressed for squid. Generally, exchanges between aggregations in pelagic invertebrates have been very poorly researched (Ritz, 1994, pp. 174–175). This study attempts to address some of the problems mentioned by Hilborn (1991) and proposes some novel uses of and approaches to the marking of squid and possibly fish. As used in this

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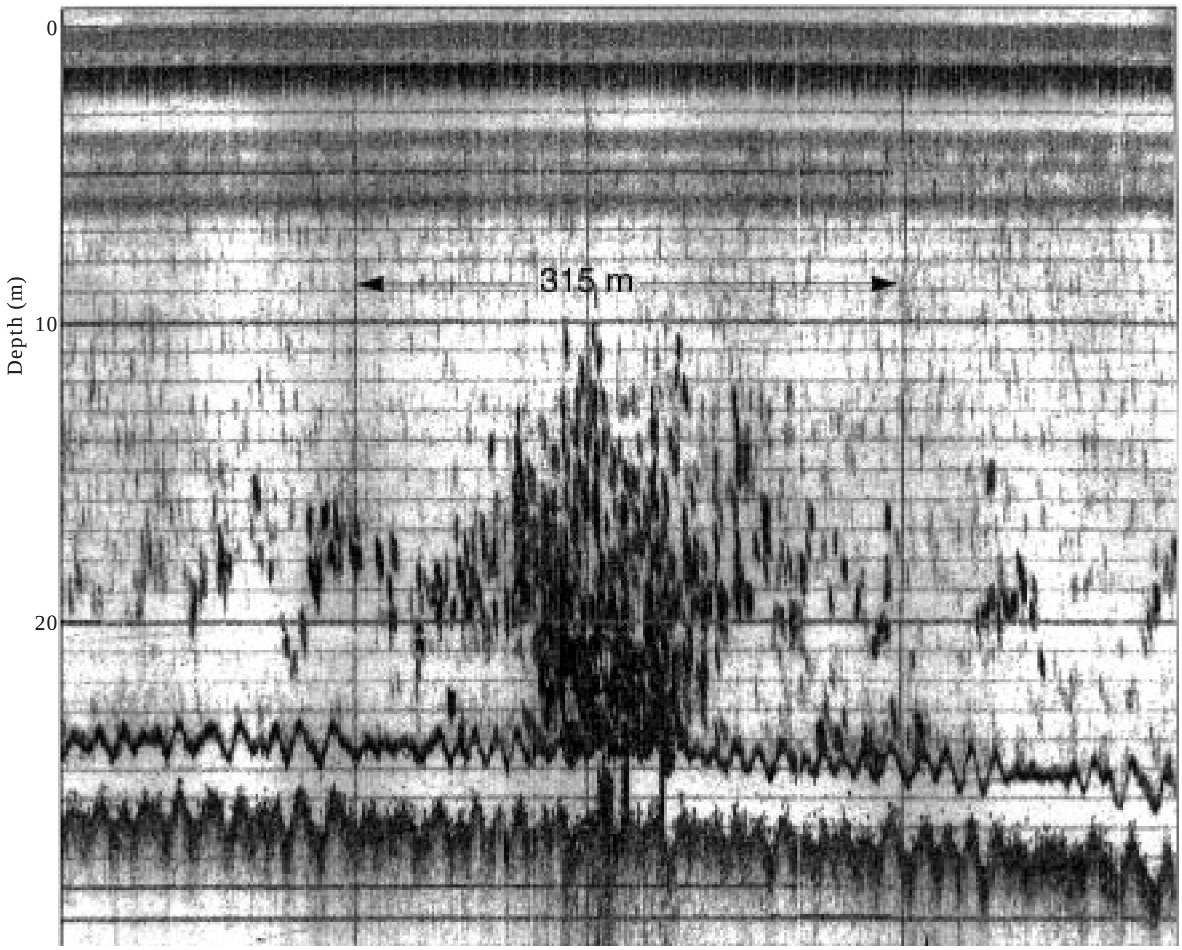

Figure 1. A mushroom-shaped spawning squid concentration, based on hydroacoustic observations.

paper, the descriptive phrase ''net stability of the concentration'' refers to the net result of the immigration of individuals to and emigration from the concentration in relation only to their original number and without reference to individuals. ''Overall stability'' refers only to individuals remaining in the concentration after n days. This is difficult to determine, because each observed concentration may contain up to four components: ''settlers'', ''immigrants'', ''emigrants'' and ''immigrant-emigrants'' (i.e. there may be multiple re-entries during any given observation period; Sauer *et al.*, 1997).

Material and methods

General

The experiment was conducted on a typical ''mushroom-shaped'' stationary spawning concentration (Sauer *et al.*, 1992, Figs 3 and 4) located acoustically (Fig. 1) and confirmed by SCUBA diving. Squid in the concentration were marked with both single and double tags (B type of the filament tag, described by Takami and Takayanagi, 1991) and immediately released on 9 and 10 November 1993. During the course of the following week, squid from the concentration were tagged on a further two occasions (11 and 12 November), and three large catches were made from it, two with an Engels 308 midwater trawl from FRV ''Algoa'' (12 and 17 November), and one with a purse seine deployed from the purse seiner ''Rietvlei'' (15 November). Catches were made at exactly the same position, marked with a buoy.

Details of the gear are given in Lipinski (1994), but positions given in that paper for trawl catches are the gear launching positions and not the positions of the actual catch.

The location of the concentration in Kromme Bay is shown in Figure 2. Each catch was carefully sorted to recover tags. Stomach contents of potential squid predators (selected from the catch) were also investigated, to check for the presence of the tagged animals.

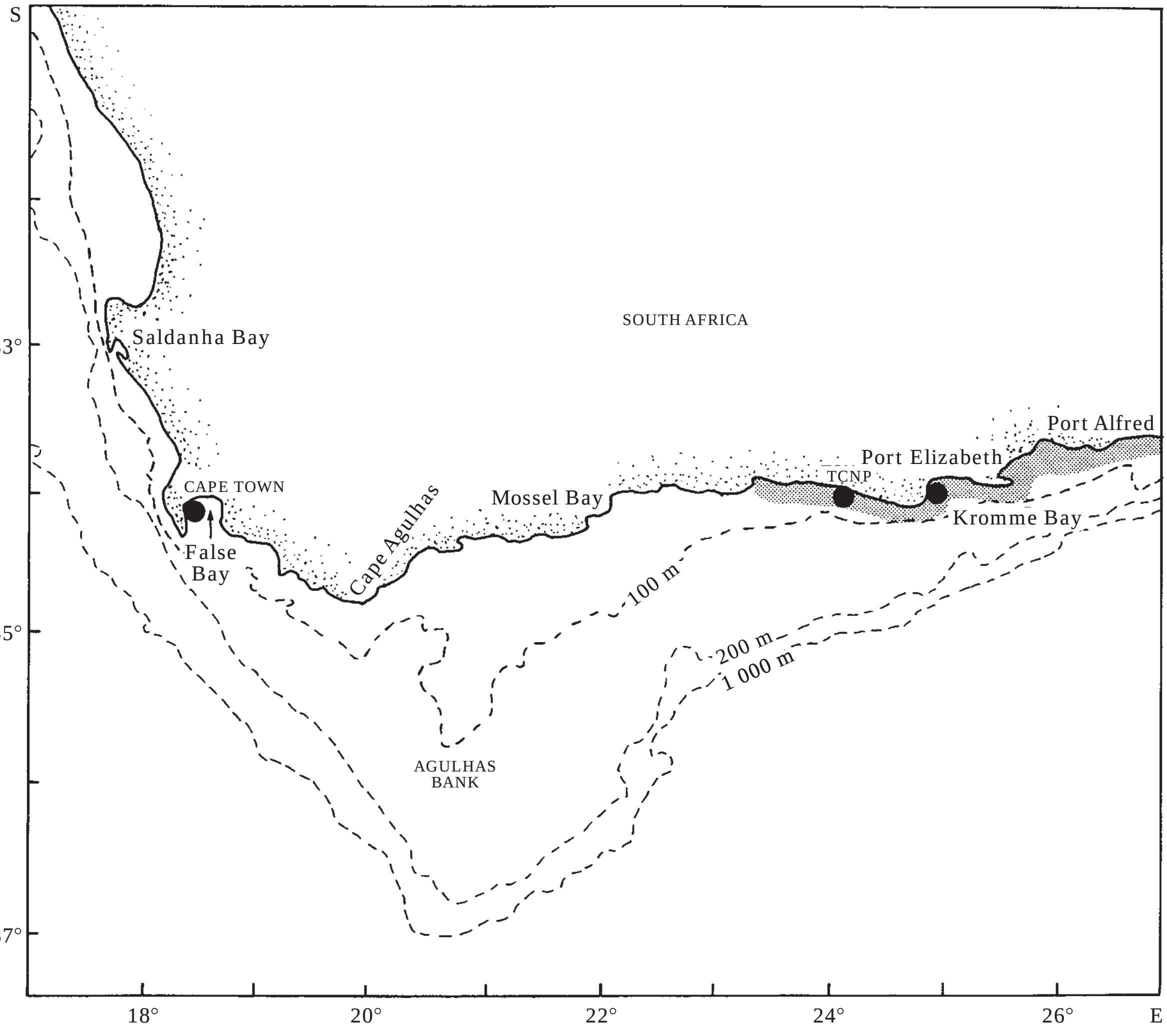

Figure 2. Sampling positions. Station near Cape Town: False Bay; station near Port Elizabeth: Kromme Bay; station in the middle: Tsitsikamma Coastal National Park. Mottled area: main spawning grounds of chokka squid.

In each case the number of animals in the concentration was estimated acoustically. From these estimates and the number of tagged animals in the catches, estimates were made of the net daily concentration stability and subsequently, emigration from the concentration, as described below.

Description of model

The model on which the method is based assumes that during the ith day after tagging, the number of tagged squid in a concentration is reduced by a factor $S_i q_i \beta_i$, where the factors S_i, q_i, and β_i (all ≤ 1), account for losses on day i due to natural mortality, tagging mortality and net emigration, respectively. The number of tagged animals captured from an aggregation n days after tagging, t_n, is then given by:

$$t_n = T \prod_{i=1}^{n} (s_i q_i \beta_i) c/B, \tag{1}$$

where T is the number of tagged animals introduced into the population, c is the number in the catch, and B the acoustically estimated number in the aggregation at the time of the catch. Equation 1 can be written:

$$t_n = T(\bar{s}\bar{q}\bar{\beta})^n \; c/B, \tag{2}$$

where $\bar{s}$, $\bar{q}$, and $\bar{\beta}$ are the geometric means of these factors, averaged over the n days following tagging. $\bar{\beta}$ can therefore be estimated from:

$$\bar{\beta} = \text{antilog } [1/n \text{ Log } (t_n B/Tc)]/(\bar{s}\bar{q})^n, \tag{3}$$

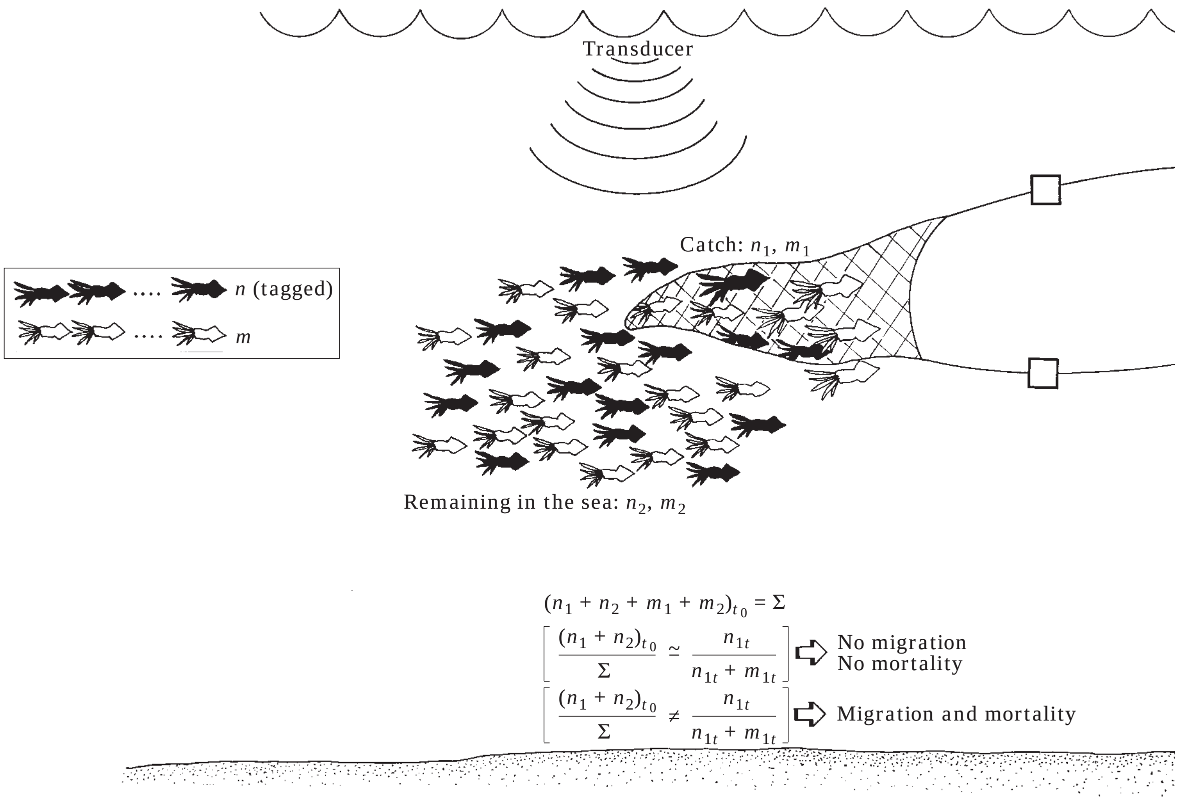

Figure 3. Principle of estimating the stability of a squid concentration. The total number of individuals (Σ) is estimated hydroacoustically and simultaneously n_1+n_2 individuals are tagged. After time t, a catch is made and n_1, m_1 individuals are counted. The net effect of migration and mortality is estimated by assessing the difference between n_{1t} expected and observed.

if estimates can be made of $\bar{s}$ and $\bar{q}$. In this study, $\bar{s}$ has been estimated from an energetics model, which provides natural mortality calculations (Lipinski *et al.*, unpublished data), and $\bar{q}$ from laboratory experiments on both single and double-tagged animals. It should be appreciated that $\bar{\beta}$ reflects the net effect of all emigration and re-entry processes occurring in one day, and that as such it should be regarded as a ‘‘net daily stability’’ factor. ‘‘Net daily emigration’’ is therefore $1-\bar{\beta}$.

A main principle on which this model is based, is illustrated in Figure 3. In generalizing the estimates of $\bar{\beta}$ from tagged animals to the concentration as a whole, it is assumed that the untagged animals in the concentration behaved in the same way as the tagged animals. It is further assumed that post-tagging survival rates for both tag types measured in an aquarium can be transposed to the field, and that they were constant throughout the period of observation.

Equation 3 was applied to both single and double-tagged animals, giving separate estimates of $\bar{\beta}$ in each case. Estimates were obtained from each of the three catches. In the case of the purse-seine catch, two separate acoustic estimates of B were used, generating two sets of $\bar{\beta}$ estimates.

Hydro-acoustic estimates of squid numbers in the concentration

The number of animals in the concentration at the time of the catches was estimated using a locally-designed echo-integration system (AIDA) interfaced to a 38-kHz Simrad EK400 echo sounder operating on a pulse duration of 1.0 ms. The integrator was capable of integrating to within 2 m of the bottom with a vertical resolution of 1 m, and had storage facilities enabling echoes to be reprocessed ping-by-ping. Target strength measurements were made *in situ* using locally-developed software (TARG) to analyse depth, amplitude and phase information taken from the parallel port of a Simrad ES400 split-beam echo sounder, which was also operated on a 1-ms pulse. Both sounders were calibrated by sphere to an estimated accuracy of 0.5 dB (including uncertainty in equivalent beam factor) 3 months prior to the study. A spot check of their on-axis receiving and transmitting sensitivities was carried out by sphere during the study itself. Single targets were isolated by TARG according to recognition criteria described in Barange *et al.* (1994). In brief, for an echo to be accepted as originating from a single target, its waveform had to

Table 1. Mean numbers, lengths and spacings of lines in each of the acoustic surveys of the squid concentration.

Date	N/S lines	E/W lines	N/S length (m)	E/W length (m)	N/S spacing (m)	E/W spacing (m)
12/11/1993	3	3	201	266	100	100
15/11/1993	7	3	268	321	65	70
15/11/1993	4	4	325	235	80	100
17/11/1993	2	2	229	320	229	320
17/11/1993	2	2	267	328	267	328

resemble that from the calibration sphere, and the sample-to-sample variation in angular bearing both athwart and longships had to fall within preset limits for a preset period (0.8 ms in this case). This is a method similar to that implemented in the widely-used Simrad EK500 sounder to discard multiple targets, although we have recently shown (Soule *et al.*, 1995) that the method is likely to produce positively biased estimates of target strength where densities are high and the target strength distribution broad.

The aggregation studied was located in 25 m of water, and during the day was mainly concentrated in the lower half of the water column. It was positioned over an egg bed, which on 15 November was estimated by divers to extend some 70 m in an east/west direction, and about 10 m from north to south. A preliminary acoustic survey was carried out on it on 12 November, followed by a midwater trawl. It was surveyed twice on 15 November (before and after the purse seine catch), and again on 17 November, immediately before and after a midwater trawl catch.

All surveys were conducted by day, and consisted of a set of north/south and east/west lines centred on the concentration, steamed at between 3 and 4 knots. The number of lines in each survey, and their average lengths and spacings (estimated from GPS fixes) are given in Table 1. In the preliminary survey, the lines were referenced to four marker buoys laid by GPS in a 200 × 200 m square around a buoy at the centre of the concentration. The grid clearly encompassed the centre of the concentration, although some squid were detected off the bottom outside the marker buoys. In both surveys on 15 November, the lines were run according to GPS fixes, assisted by visual reference to a single central marker buoy. Prior to the second survey, the buoy, which had to be lifted for the purse seine catch, was relaid at the centre of the concentration by an accompanying commercial squid jigging vessel, the ''Langusta''. Both surveys clearly encompassed the densest part of the concentration, and there were few indications of squid outside either grid. The same positioning technique was used for the two surveys on 17 November, which both consisted of two north/south and two east/west lines around a central marker buoy. In this case there were insufficient lines to establish whether the entire concentration had been encompassed.

Density estimates were made for each survey from the weighted (by length) mean density per line. Sampling variances were estimated from the variation in density per line, with appropriate weighting for differences in line length (Jolly and Hampton, 1990). The variance estimator is unbiased if the lines are randomly spaced, otherwise it is positively biased (Jolly and Hampton, 1990). Although the lines were not random by design, it is assumed that difficulties in keeping the ship on course introduced sufficient randomness in transect spacing to have made the variance estimator reasonably unbiased. Aggregation biomass was calculated from the mean density and the survey area, which for the first three surveys was taken as the product of the mean line lengths in the two directions, to each of which was added the mean line spacing in that direction to allow for squid at the edges of the grid. For the two surveys on 17 November, where there were too few lines to establish the extent of the concentration, the area was taken as the mean of the estimates on 15 November (0.133 km^2).

A mean target strength for converting back-scattering strengths to density was taken from a single experiment at 1830 hours on 11 November, which was the only experiment in which the squid were considered to be sufficiently dispersed to give unambiguous estimates of target strength (see Results). The measurements were made while at anchor on the concentration.

The mean mass of individual squid in the concentration was taken from the purse-seine catch, which Lipinski (1994) concluded gave the least biased sample of the size distribution.

Natural survival of squid (estimation of $\bar{s}$)

Natural survival (per day) of squid was taken from Lipinski *et al.* (unpublished data). It was calculated from the formula $P_a = 1/P_s b$, where P_a – total (summary) survival of adult squid, P_s – total (summary) survival of squid paralarvae and b – fecundity. P_s was calculated as 0.000542, using a computer simulation (Lipinski *et al.*, unpublished data). Fecundity b was assumed to be on average 13 000 (W. de Wet, 1995 and pers. comm.).

Total P_a was then calculated as 0.142 (s = 0.99 per day, for 300 days). To calculate the total survival (natural and tagging), P_a was multiplied by the tagging survival calculated as a result of aquarium experiments.

Post-tagging survival (estimation of $\bar{q}$) and a possible tag loss

Post-tagging survival and tag loss were investigated in an aquarium maintenance experiment. Squid were hand jigged in False Bay (Fig. 2) and transported overland to aquaria. Six batches of squid (together consisting of 131 individuals) were maintained for varying periods of up to a month between March 1992 and December 1993. Aquaria were 2 m in diameter and 1.5 m deep, covered by netting and sheets of black plastic. A semi-open water system with a retention tank and sand filtration was used.

Squid were fed on live mullet *ad libitum* once a day. Daily maintenance of tanks included cleaning, checking water flow and aeration and recording temperature. Each experiment consisted of an experimental and control group in identical aquarium settings and subject to the same maintenance procedures.

On arrival at the aquarium, an experimental group was tagged either with spaghetti tags in the anterodorsal part of the mantle (first two batches) or with filament tags in one of the fins. Spaghetti tags have been used for tagging *Illex illecebrosus* in Canadian waters (O'Dor *et al.*, 1979; Hurley and Dawe, 1980). The filament tags were recommended for *Loligo* by Kawano (pers. comm.) and have been widely used in Japanese tagging programmes (Takami and Takayanagi, 1991; Nagasawa *et al.*, 1993).

Tag loss was also investigated in the field in November 1993, when field trials were conduced in St Francis Bay (742 squid tagged) and in the Tsitsikamma Coastal National Park (TCNP) (200 squid tagged) (Fig. 4). Squid were caught by means of hand jigging, tagged on both fins with filament tags, injected with OTC and released. Both tagged and untagged squid were directly observed below the commercial squid jigging vessels within 8 hours of tagging, in order to observe behaviour after tagging and address the question of possible reduced probability of recapture of tagged individuals.

Aquarium maintenance gives only a very rough estimate of post-tagging survival. It was assumed that aquarium maintenance survival is determined by two variables, q_1 or q_2 and the aquarium-specific fraction of survival, a. The last is highly variable and depends on water quality, temperature and other factors, and assumes that the condition of animals on arrival is perfect. It was further assumed that the effect of a is negligible in the first 1–4 days of maintenance (Fig. 4). Also, $q_1/q_2 = q_1a/q_2a$. On that basis, the maximum q_1 or q_2 for the field-tagging calculations was estimated from aquarium maintenance experiments, as follows:

$$q_1 = \left(1 - \frac{m_1}{r}\right)^{\frac{1}{n}}$$

for single-tagged animals, and

$$q_2 = \left(1 - \frac{m_2}{r}\right)^{\frac{1}{n}}$$

for those tagged with double tags, where m_1 and m_2 are the numbers of deaths for single- and double-tagged squid, respectively, for the period n (number of days); and r is the number of squid initially introduced into the aquarium. The loss of tagged animals to predators was investigated by collecting stomach contents of various predators where possible, and observing predation *in situ*.

Results

Estimation of model parameters

Parameters n, c, T and t are given in Table 2. Results of the biomass estimates are presented below.

The mean target strength (TS) used in all of the biomass calculations was -42.5 dB kg^{-1}, which was estimated from TS data collected at about 1830 hours on 11 November, and the mean mass of squid in the purse seine catch (0.30 kg). The TS distribution for this experiment is shown in Figure 5(c), which shows a clear unimodal distribution, peaking at -48 dB per individual. Shown in Figure 5(a) and (b) are TS distributions obtained for the same aggregation earlier in the day, at around 1440 hours and 1700 hours respectively. It can be seen that the peak around -48 dB is absent from Figure 5(a), and is only noticeable as a secondary peak in Figure 5(b). The major peak around -38 dB per individual in these two figures is attributed to multiple targets, which Barange *et al.* (1994) have shown are often not excluded by the phase-stability criterion, causing TS to be severely over-estimated when densities are too high. (Similar spurious peaks were found in all other TS experiments conducted by day during this study.) The development of the peak around -48 dB in Figure 5(b) and (c) appears to indicate a lowering of density towards nightfall, on the grounds of which the distribution in Figure 5(c) was chosen as the most reliable. This choice is also supported by the fact that the mean TS kg^{-1} of -42.5 dB from this experiment agrees well with that obtained by Jefferts *et al.* (1987) for the TS of *Loligo opalescens* at 120 kHz (-42.3 dB kg^{-1}) and with the value of -41.1 dB kg^{-1} obtained by Arnaya *et al.* (1989) for the TS of *Todarodes pacificus* at 28.5 kHz.

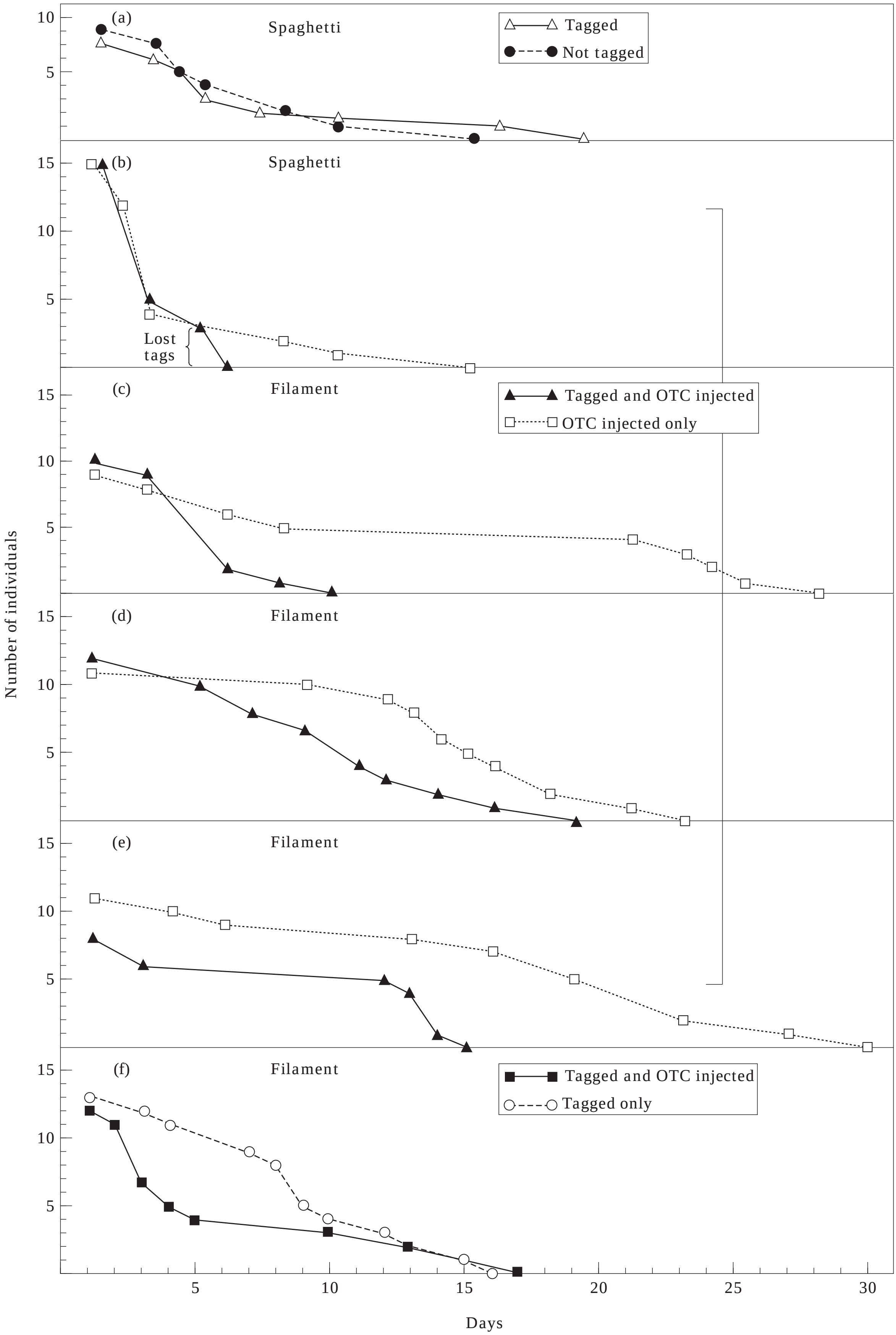

Figure 4. Squid survival during aquarium experiments. Spaghetti tags were used in a, b; filament tags in c–f. Data from the last experiment were used in the calculations because this experiment most closely resembled tagging in the field.

Table 2. Parameters necessary to calculate net stability of the squid concentration. Values in parentheses are the percentage of tags in the catch.

Tagging date	T_1 (single)	T_2 (double)	MWT1 (12/11/1993) n (days)	MWT1 (12/11/1993) c (number caught)	MWT1 (12/11/1993) t_1 (single tags recovered)	MWT1 (12/11/1993) t_2 (double tags recovered)	Purse seine (15/11/1993) n (days)	Purse seine (15/11/1993) c (number caught)	Purse seine (15/11/1993) t_1 (single tags recovered)	Purse seine (15/11/1993) t_2 (double tags recovered)	MWT2 (17/11/1993) n (days)	MWT2 (17/11/1993) c (number caught)	MWT2 (17/11/1993) t_1 (single tags recovered)	MWT2 (17/11/1993) t_2 (double tags recovered)
9-10/11/1993	1423	—	2.5	5131	31 (0.60%)	—	5.5	20 915	115 (0.55%)	—	7.5	3414	3 (0.09%)	—
11/11/1993	—	149	<1		—	3	4		—	9 (0.04%)	—	—	—	—
12/11/1993	—	148	—	—	—	—	3		—	19 (0.09%)	—	—	—	—

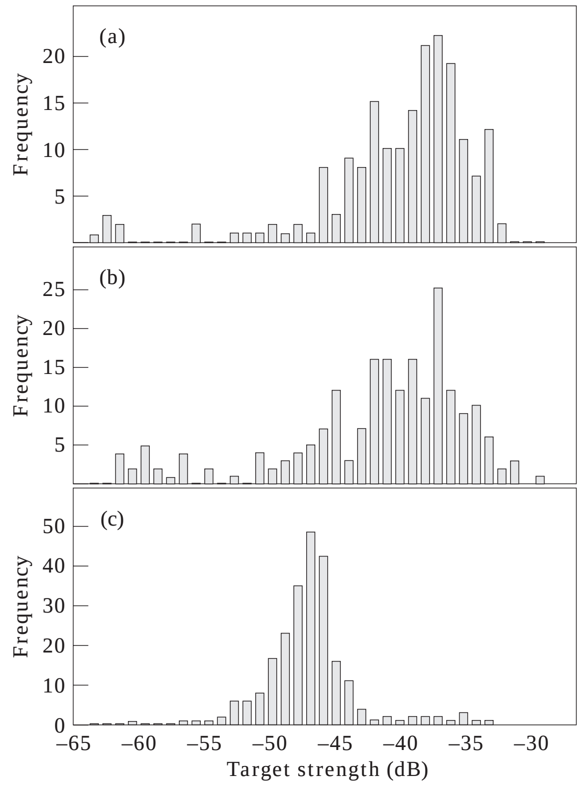

Figure 5. Squid target strength distributions from *in situ* experiments on 11 November 1993: (a) in the afternoon; (b) at dusk; (c) at night.

Estimates of mean density, aggregation biomass for the surveys and their estimated CVs, are set out in Table 3. It will be seen that the estimates vary widely, even in repeated surveys on the same day, but that all estimates are of the order of tens of tons.

Estimation of post-tagging survival per day and tag loss

During the aquarium maintenance experiment, 1 squid was lost during the first 3 days from the group of 13 squids tagged with 1 filament tag; therefore $q_1 = (1 - 1/13)^{1/3} = 0.9736$ (see Fig. 4(f)). For the squids tagged with two filament tags and injected with OTC, one squid was lost during the first 2 days from the group of 12; therefore $q_2 = (1 - 1/12)^{1/2} = 0.9574$ (see Fig. 4f).

For the two aquarium experiments conducted with spaghetti tags, three of the squid from the tagged and OTC-injected group lost their tags after 3–4 days. There were no field trials for the spaghetti tags. For the filament tags, both the aquarium experiments (up to 18 days) and field trials (up to 20 days, 63 squid recovered) revealed no tag loss.

At one spawning site, five tagged squid were observed and recorded on video camera in the field within 24 hours of tagging. No obviously abnormal behaviour was observed. All tagged squid sighted were males, four of which were paired with females. One of the paired males successfully defended his female against other intruding lone males in the vicinity. Feeding behaviour as evidenced by attacks on jigs appeared also not to be affected: tagged squid were often immediately recaptured. There was no evidence that predators attack tagged animals more readily; no tagged animals were found in stomach contents of predators (fish, sharks and rays) and no attacks on tagged animals were observed during diving.

The results of recaptures of tagged squid in the field (Figs 6 and 7) strengthen the assumption that there were no differences between the post-tagging distributions of single- and double-tagged squid and that their recapture patterns (linked to survival) were similar.

Quantitative concentration stability: results of the model

The results of the calculations of $\bar{\beta}$ (Table 4) are remarkably consistent. They range from 0.7080 to 0.8479 per day (s.d. 0.0544, mean 0.78). It should be noted that these results are quite robust to changes in the biomass estimates, already pointed out in the Material and methods section.

These results indicate that approximately 80% of the initial number of individuals remain in the concentration

Table 3. Estimates of mean density and biomass of squid concentration from each of the acoustic surveys

Date	Mean density (gm^{-2})	Area (km^2)	Biomass (tons)	CV (%)
12/11/1993	246	0.110	27.1 (91 417)*	50
15/11/1993	190	0.130	24.7 (83 321)*	30
15/11/1993	150	0.136	20.4 (68 816)*	34
17/11/1993	504	0.133	67.0 (226 013)*	29
17/11/1993	273	0.133	36.3 (122 452)*	30

*Numbers of individuals given in parentheses.

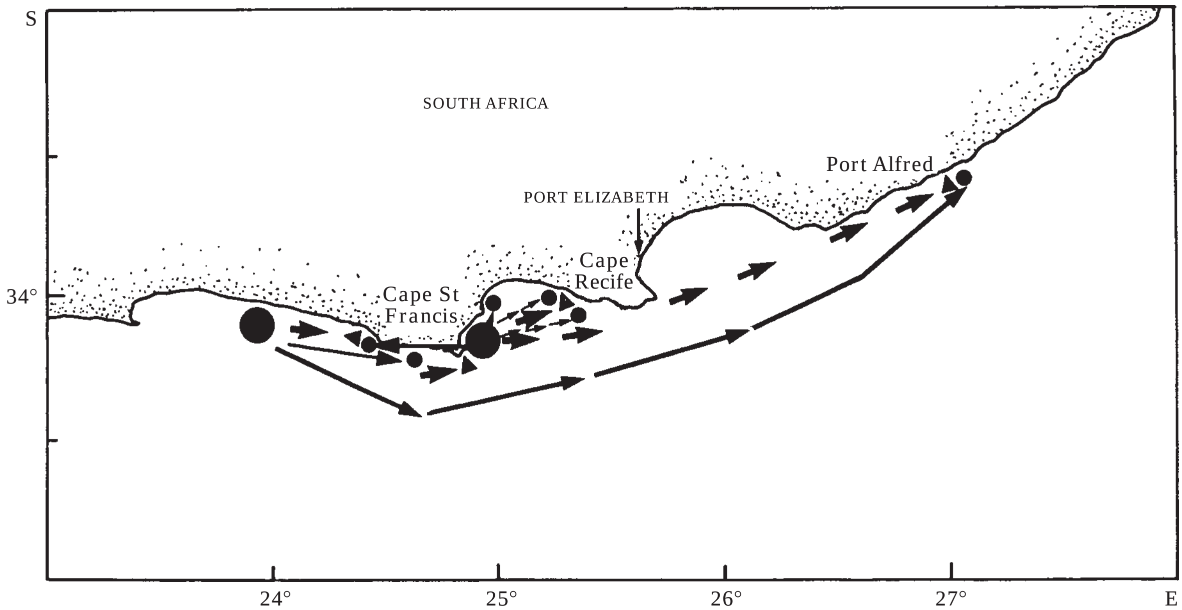

Figure 6. Comparison of migration by single- and double-tagged squid. Large dots: tagging sites; short and thick arrows and triangles: simplified migration routes and recapture sites of single-tagged squid; long and/or thin arrows and small dots: simplified migration routes and recapture sites of double-tagged squid.

per day. Obviously, there may be new individuals (immigrants) in this number, or re-entering individuals (emigrants–immigrants). The rest (20% per day) emigrate from the concentration (e.g. >7.2 tons of squid from >36 ton concentration).

Discussion

Acuracy of $\bar{\beta}$ estimates and potential improvements

In the present study an attempt was made to investigate and, where possible, take account of most of the sources of potential error in tagging studies (Ricker, 1975). Nevertheless, potential error in estimating model parameters remains large and there is a need for improvement.

Biomass

The greatest source of uncertainty in the biomass estimates is in the estimate of target strength used to obtain them. Although the results from the TS experiment are reasonably convincing *per se*, the validity of applying a night-time TS estimate to survey data collected by day is doubtful. There could, for example, be large diel differences in mean TS due to differences in orientation, and possibly the size composition of the animals. Ideally, biomass estimates should be based on TS data collected simultaneously with the echo-integration data to account for local variations in TS, but the inability of the present system to isolate individual echoes successfully during the day precluded this. It is hoped that an improved single-target-recognition system, now under development, will enable reliable TS estimates to be collected by day in future.

Significant error could also have been introduced through the estimates of area. Recent experiments with a differential GPS in the region suggest that the line lengths in Table 1 could have been in error by as much as 50 m due to errors in GPS fixes. The net effect on the calculated survey areas should, however, not have been large, because these errors would have tended to be random. Errors in allowing for edge effects, and those arising from the assumption that the surveys all encompassed the concentration completely are likely to have been more significant. The reason for the latter is that, despite the centre of the concentration being intersected on all of the surveys, some squid were detected on all but two of the outermost lines.

Other sources of error worth noting are the 0.5 dB calibration uncertainty (equivalent to 12%), and the possibility that there were substantial amounts of squid within 2 m of the bottom, where they would not have been recorded acoustically.

Survival

Survival rates are potential sources of large errors. As pointed out by Lipinski *et al.* (unpublished), natural survival $\bar{s}$ calculations are always made under a number

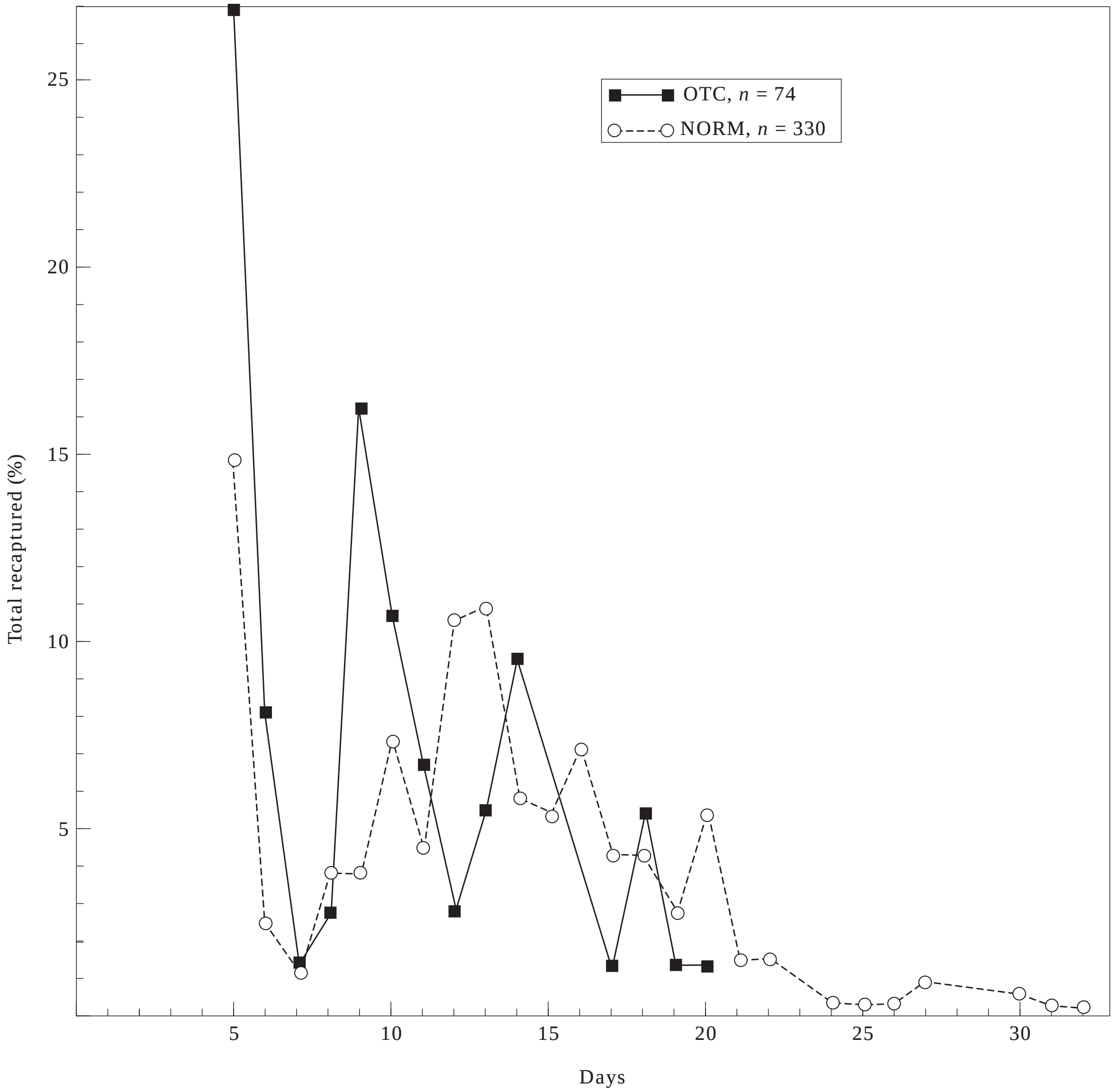

Figure 7. Comparison of recapture patterns in single- and double-tagged squid. X-axis: days at large; y-axis: percentage of total number recaptured in each category.

of assumptions. Its application is also subject to large error, as it is always assumed that $\bar{s}$ is constant throughout the period of application, which obviously does not hold. Quantification of these errors and possible methods of improvement are, however, beyond the scope of this paper. The estimation of tagging-related decrease in survival $\bar{q}$ also includes the risk that aquarium-derived $\bar{q}$ may not be applicable to the field environment. This especially concerns predation, which cannot be simulated in the aquarium observations. The fact that no predation on the tagged squid was recorded so far (e.g. Smale *et al.*, 1995), is not a definite proof that tagging is irrelevant in this regard.

If $\bar{s}$ or $\bar{q}$ were higher than assumed in the present paper, $\bar{\beta}$ would have been very slightly under-estimated. If they were slightly lower, it would have made almost no difference when the number of days of observation (n) is small. They would have some impact if they were substantially lower and/or n is large.

Fortunately, $\bar{s}$ and $\bar{q}$ have a slight impact on the calculation of $\bar{\beta}$. The short period of observation further contributes to their low significance, in a similar manner to the situation described by Hilborn (1991).

More important parameters in terms of their potential impact are the number of tags recovered (t) and the period of observation (n).

Table 4. Parameter B necessary to calculate net stability of the squid concentration (β) and result of these calculations

Tagging date	Tag	Catch identification	B*	β
9-10/11/1993	Single	MWT1	91 417	0.71
		Purse seine	83 321	0.85
			68 816	0.82
		MWT2	226 013	0.81
			112 452	0.75
11/11/1993	Double	Purse seine	83 321	0.74
			68 816	0.71
12/11/1992	Double	Purse seine	83 321	0.84
			68 816	0.79

*Note: for various B estimates refer to Table 3.
$q_1=0.97$, $q_2=0.95$, $s=0.99$.

Number of tags recovered

If a significant number of tags was missed during sorting of the catch, $\bar{\beta}$ would have been underestimated. This is considered to have been unlikely, because many people thoroughly sorted each catch. The percentage of tags missed in the packing factories, however (Sauer *et al.*, unpublished) depended on the efficiency of individual sorters and may have been as high as 12%.

Another important source of error is tag loss, which obviously may affect recoveries (O'Dor *et al.*, 1979; Kawano *et al.*, 1986 and pers. comm.). In the relevant period (up to 20 days) there was no observed tag loss, either in the aquaria or in the field. However, even if a large number of tags had been lost, the main conclusion of the present work would not have been affected.

In situ observations indicate that filament tags do not preclude squid from swimming normally, forming pairs, copulating, spawning or capturing jigs again. This is in sharp contrast with the observations of O'Dor *et al.* (1979), who observed that tagging seriously affected *Illex illecebrosus* swimming ability and behaviour.

Duration of observation

This is a critical parameter in the study. Lack of accuracy may have caused some error: duration of observation was measured in days and rounded off to one date if the consecutive tagging sessions were less than 12 hours apart (usually an evening of one day and early morning of the next day). In the present study the number of days over which stability was measured was, however, small (up to 7.5); with an increase in n, error related to accuracy would increase and may become a serious problem.

Interpretation of $\bar{\beta}$ estimates

In studies of this kind, the proper formulation of its aims, the marking plan and the techniques used largely determine the quality of results (Nielsen, 1992). The methods used in the present study (e.g. the type of tags used) were conventional, but the main aim of the study and the marking plan were rather unusual. Most tagging studies investigate the migration routes and/or abundance (biomass) of the stock, without paying much attention to investigation of the underlying assumptions. During the course of the present study possible sources of error in the conventional application of tagging were investigated and the most important of them, migration, singled out. In his work on the estimation of animal abundance, Seber (1982) did not mention any technique of stock assessment that allows for emigration and immigration being both unrestricted and variable. This is an unfortunate shortcoming of all tagging studies conducted in the open ocean (Hilborn, 1991).

The present study demonstrated that migration associated with squid spawning aggregations is a highly dynamic process, in this particular case involving an average of at least 20% of the concentration per day in 7.5 days of observations. Therefore, ideally, these dynamics should be incorporated into models used for estimating spawning biomass.

Future studies should determine the variability of these dynamics and patterns associated with it in various circumstances. For example, it would be useful to investigate the dispersal rates of the concentration, the duration of development and of dispersal, and average squid density between concentrations along various migration routes. To the best of our knowledge, there are no published data on these processes in cephalopods.

The present study did not provide for the quantification and dynamics of either immigration or emigration. Squid may move in and out of concentrations (Sauer *et al.*, 1997), which complicates calculation of the net stability factor (calculated as 0.8 in this study). Another more difficult problem concerns the long-term spatial dynamics between various concentrations and individuals outside the spawning areas, possibly still in feeding aggregations (Sauer *et al.*, 1992). This is particularly difficult to investigate, because tag returns are only made from the fished pool; the stability of spawning aggregations over longer periods than investigated in the present study and the extent of migration to areas outside of those where fishing operations take place are unknown.

It should be appreciated that the results presented here apply only to that part of the population which concentrates on the inshore spawning grounds in summer and that the dynamics of non-spawning aggregations, as those of further offshore, may be very different.

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