A correction factor for, and its application to, visual censuses of littoral fish

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Visual estimation techniques were used between October 1976 and May 1977 on the fish fauna of an enclosed mid-intertidal pool in the eastern Cape, South Africa, to test the usefulness and accuracy of this non-consumptive census method. In January, 1977, two pools were censused for fish, then poisoned using the ichthyocide 'pronoxfish' and all fish collected. Forty species in 21 families were obtained from the two stations. The accuracy of visual estimates varied with the species of fish. Secretive and cryptically coloured types, as well as species which inhabit crevices, were underestimated, between 0 and 86% being counted. Other fish with protective colours but that occur more openly and do not react adversely to divers, as well as schooling species, were also underestimated, but up to 100% of the total were observed. Those which occur singly or in small groups in the water column were counted more accurately, with 57 to 100% of the actual number being seen. Correction factors were calculated from these data and applied to a census taken of one pool in May. Comparisons of corrected and actual numbers indicate that these factors were relatively accurate for non-secretive species. The factors will, however, vary for each species, from observer to observer, depending on their personal experience, and from area to area.

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Visuele skattingsmetodes is toegepas op die visfauna van 'n ingeslote tussengetypoel In die Oos-Kaap, Suid-Afrika, van Oktober 1976 tot Mei 1977, om dle nut en akkuraatheid van dié nie-vernietigende metode te bepaal. 'n Opname van vis in twee poele is gedoen in Januarie 1977, en daarna is die poele vergiftig met die visdoder 'pronoxfish' en die opbrengs is versamel. Veertig spesies behorende tot 21 families is op dié manier gevind. Die akkuraatheid van visuele skattingsmetodes het met die verskillende spesies vis gewissel. Sku en kripties gekleurde spesies, sowel as dié wat rotsskeure bewoon, is onderskat, met slegs 0 tot 86% getel. Ander visse met kamoeflering, wat nie so sku is nie en nle ongunstig reageer op die teenwoordigheid van duikers nie, sowel as spesles wat in skole voorkom, is ook onderskat, maar tot 100% van die totaal is waargeneem. Dié wat enkel of in klein groepies voorkom is meer akkuraat getel, en 57 tot 100% van die werklike getal is waargeneem. Korreksiefaktore vir hierdie gegewens is bereken en toegepas op die resultate van 'n opname gedoen op een poel in Mei. Vergelykings tussen aangepaste en werklike getalle dui aan dat hierdie faktore relatief akkuraat is vir spesies wat nie sku is nie. Die faktore sal egter varieer van spesie tot spesie, van gebied tot gebied, en van waarnemer tot waarnemer, afhangende van persoonlike ervaring, S.-Afr. Tydskr. Dierk. 1981, 16: 73 - 79

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In order to estimate the composition and relative numbers of a given biota - a prerequisite to an understanding of many ecological relationships - visual census techniques have, in the past, been widely employed (e.g. mammals, birds). It is only recently that such techniques have been applied to fish, usually in conjunction with data gained by more conventional methods such as spearfishing or poisoning (Smith & Tyler 1972, 1973, 1975; Emery 1973). Visual censuses tend, however, to yield lower estimates than the number actually present (Holmes, McKenzie, Petersen & Grant 1968). Sampling techniques such as poisoning, particularly when used in open systems such as coral reefs, may also be quantitatively inaccurate. This is due to four main factors: (1) variable susceptibility of the fish to the poison, (2) water currents removing the poison before the full effect takes place, (3) immigration/emigration to and from the area being sampled, and (4) subsequent immigration of predators unaffected by the poison which then feed on the dead fish before they can be collected.

The problems that affect poison collections can be overcome if the area sampled is isolated. This can be partially achieved by enclosing the area with nets (Randall 1963; Quast 1971), although this will only solve the latter two problems. It was therefore decided to use an intertidal pool as it represents a naturally closed system with the added advantages that no currents occur which can remove the poison, which thus remains in the sample area for a long enough time period to kill all fish. This includes those which are least susceptible, the muraenids (Randall 1963). Comparisons of estimated (visual census) and actual numbers present (poison collection) can then be made to quantify the amount of error involved in such counts. A correction factor was calculated and the predictive power tested by use in the field. The effects of substrate and cover types, water turbidity, light conditions and other physical features on this factor were not determined.

Methods

Study areas

Two pools of comparable size were used for this study. They are typical of the large, deep pools that occur in the lower intertidal zone at irregular intervals along the coast. Recorded temperatures in the two pools ranged from about 15 °C in winter to about 27 °C in summer. The first pool (Pool 1) is at Clayton's Rocks in the eastern Cape $(33^{\circ}31'54''S/27^{\circ}04'44''E)$ (Figure 1). It is a rock pool about 12×4 m, with a depth of 3 m at low tide. The sides of the pool are vertical and covered by a short algal turf of corallines and *Hypnea spicifera*. The substrate consists of rounded stones and rocks with the exception of the shallow southerly portion where a coarse sand predominates. The southern and western sides of the pool fall deeply to the maximum depth. The western half of the southern rockface forms a crevice 5,5 m long where it meets the bottom and this rises at an angle of about 30° to the surface at the western entrance. The crevice is about 0,6 m deep and 0,6 m high at the base, but narrows markedly towards the top, being about 30 cm deep and 3 cm high.



Fig. 1 The study areas in the eastern Cape Province, South Africa. Adapted from Topographical Chart 3326, Grahamstown.

The second pool (Pool 2) is located some 4 km further west, at Black Rock (33°33'30''S/27°00'39''E), and is of approximately the same size and depth as Pool 1. The north-eastern edge has a similar, though deeper (up to 1 m), crevice at its base. The algal cover was about three times thicker than in Pool 1 when assessed using the technique described by Massey (1976), being dominated by *Sargassum* spp., *Ulva* sp. and *Hypnea spicifera*. The substrate was mainly fine sand with the exception of the southern edge which was a sandstone bedrock with some covering of mollusc shells.

Direct observations

The general habits and habitats of fish in the pools of the mid-intertidal zone were observed using SCUBA and by snorkeling from January 1975 to January 1977 at twoand four-week intervals. This thorough knowledge of the fish and their habits was found to be essential in order to make accurate identifications and visual estimates.

Visual censuses of Pool 1 were initiated in October 1976 and these were conducted exclusively with SCUBA (Table 1). Each census was made separately by two divers and consisted of four to eight slow round trips. This is possible as tide pools are enclosed and this method

 Table 1
 Summary of the main features of the seven visual censuses and three collections

Pool	Time	Date	Census type	Horizontal visibility (m)
1	12h45 — 14h05	28.10.76	Visual	1,2
1	09h30 - 10h20	21.11.76	Visual	2
1	09h40 - 10h20	7.12.76	Visual	1,5
1	09h30 10h20	20.01.77	Visual	2
1	10h20 – 12h40	20.01.77	Poison collection	2
2	10h15 10h45	21.01.77	Visual	3
2	10h50 - 12h10	21.01.77	Poison collection	3
1	13h10 – 13h40	21.01.77	Visual	5 - 6
1	11h10 - 11h50	24.05.77	Visual	4
1	11h50 - 13h30	24.05.77	Poison collection	4

therefore results in a thorough census with as little as possible being overlooked. Thus, it allows a diver several opportunities to recount schooling species and observe secretive types that may have been missed on a previous round trip. The fish were counted and recorded *in situ* on an underwater slate, each complete census taking between 20 and 30 min to complete. The mean number of the estimates of common species as well as the highest number of the rarer types was recorded for laboratory analysis. The latter are defined as those which are secretive and/or cryptically coloured and which may therefore be missed by the second diver due to their having been scared into cover. In support of this assumption, it was noted that the first diver always recorded the same or higher numbers of such fish species.

Collection of fish

The ichthyocide 'pronoxfish' was used and applied after the divers felt that the consistency of their estimates made on each round trip of the pool was such that no fish had been missed. Immobilized fish were collected before the tide entered the pool so as not to allow any uncounted fish to enter. It was judged that all dead fish had been collected when three round trips, lasting about 7 minutes each, produced no additional specimens. The fish were preserved in 10% formalin and subsequently identified to species level in the laboratory.

Sample analysis

The results were analysed with respect to relative abundance and coefficients of variation. The relative abundance index is calculated as the percentage of the total number of individuals counted that belong to a particular species (Hobson 1974). In the present study, it was determined only for the visual censuses as its main use is an indicator of the species most likely to be seen in a particular habitat. The degree of variability between successive censuses was determined by calculating the coefficient of variation for five counts of Pool 1. This is the percentage that the standard deviation of the mean number of animals counted represents of that mean (Sokal & Rohlf 1969).

Results

Visual censuses

Gibson (1969) divides the littoral fish fauna into four groups - true and partial residents, seasonal and tidal visitors. Of the 18 fish species observed in Pool 1 between October 1976 and January 1977, only 6 occurred in all 5 censuses and have coefficient of variation (CV) values below 100% (Table 2). These six species have been noted on almost all dives made in the lower intertidal region and can therefore be classed as partial residents as their distribution also extends below low water. The only true resident observed in Pool 1 is Cafrogobius caffer which has a high CV value (105%). Analysis of supplementary data from further up the tidal column, however, gave much lower CV values (28%). This is to be expected as it was only observed in the shallow water at the edges of deep low-level pools, being the most abundant species further up the littoral zone. Therefore, although it is an intertidal resident, the high CV value shows clearly that its preferred habitat is not deep pools.

The remaining 11 species have CV values of over 100% and all are seasonal visitors. In order to encompass all seasonal species in the eastern Cape area, this group needs to be redefined to differentiate between seasonally occurring juveniles and adults which move into the littoral for breeding purposes. The latter was the group which was originally classified by Gibson (1969) as seasonal visitors. The former group is here defined as juveniles which are resident seasonally in the intertidal zone and will be classified as 'seasonal-residents'. Their CV values are lower than 100% during the months that they occur, but in a year-long census, CV values would rise to over 100%. None of the species censused were tidal visitors as the visual censuses were taken at low tide. This group of fish moves into the littoral to feed at high water.

The resident and visitor classes defined by Gibson (1969), as well as the seasonal residents defined above, can thus be grouped by CV values as those that are below and above 100%. This arbitrary limit was selected on the basis of an analysis of 22 poison stations taken in the eastern Cape. Further subdivision has to be based on a knowledge of the ecology of each individual species. This method is very similar to the variability index used on birds which is calculated as the percentage that the standard error (SE) constitutes of the mean (Davis 1942). The CV was used in preference in the present case, however, as the standard deviation shows the population range whereas the SE gives the error of the mean (Sokal & Rohlf 1969).

Calculation of correction factors

The accuracy of two visual censuses was tested by comparing them to the results of poison collections taken subsequently (Table 3). The correction factors (Cf) were calculated from this data as:

$$Cf = \frac{100}{\overline{x}}$$

where \bar{x} is the mean percentage accuracy of the visual estimates for that species or group of fish. The estimated number in any subsequent visual census is then multiplied by the relevant factor to obtain the corrected census value.

In the present case, 37 fish species in 19 families were collected and these could be classified into four groups (Figure 2, Table 4) defined below:

Secretive species — fish which are either nocturnal or shy and retire into weeds, sand, crevices, caves or other cover on the approach of divers. They were heavily underestimated, with 0 to 2,4% ($\bar{x} = 0,2\%$) being observed in the present case. Included in this group are the muraenid and

Family	Species	Number (mean)	Coefficient of variation (CV)	Range of relative abundance
Ariidae	Tachysurus feliceps*	1,0	224	0 - 2
Atherinidae	Juveniles	12,8	207	0 - 6
Serranidae	Epinephelus guaza*	1,8	107	0 - 2
Sparidae	Diplodus cervinus	8,2	16	0,8-4,2
	Diplodus sargus	399,0	64	62,2 - 92,0
	Lithognathus lithognathus	0,8	224	0 - 1,6
	Rhabdosargus holubi	5,2	58	0,2-2,4
	Sarpa salpa	3,8	183	0 - 3,4
	Sparodon durbanensis	1,2	149	0 - 0,4
Mullidae	Pseudupeneus pleurotaenia	0,4	137	0 - 0,2
Chaetodontidae	Chaetodon marleyi	0,2	224	0 - 0,2
Cheilodactylidad	e Chirodactylus brachydactylus	5,2	32	0,5 - 2,4
Mugilidae	Juveniles	53,6	155	0 - 20
Labridae	Stethojulis trilineata	0,8	224	0 - 1,6
Clinidae	Clinus superciliosus*	13,4	49	1,7- 9,0
Gobiidae	Cafrogobius caffer*	0,8	105	0 – 0,6
	Gobius saldanha	2,4	23	0,2-1,2
Tetraodontidae	Amblyrhyncotes honckenii	1,0	100	0 - 1,2

Table 2Estimated density of 18 fish species belonging to 12 familiesobserved in visual censuses of Pools 1 & 2 between October 1976 andJanuary 1977

*These estimates are based on the highest number observed by individual divers.

Family			Po 20.0	Pool 1 20.01.77		Pool 2 21.01.77	
		Species	Visual	Actual	Visual	Actual	
1.	Muraenidae	Gymnothorax undulatus	_		_	1	
2.	Congridae	Conger wilsoni	-	1		9	
3.	Ariidae	Tachysurus feliceps	5	21	-	-	
4.	Syngnathidae	Nannocampus elegans	_	1	_	_	
5.	Serranidae	Acanthistius sebastoides	-	1	-	-	
6.		Epinephelus flavocaeruleus	-	-	-	1	
7.		Epinephelus guaza	5	9	3	22	
8.		Epinephelus spiniger	-	_	_	2	
9.	Kuhliidae	Kuhlia taeniurus	-	-	1	1	
10.	Pomadasyidae	Pomadasys olivaceum	-	-	4	5	
11.	Sparidae	Diplodus cervinus	7	6	8	14	
12.		Diplodus sargus	160	137	126	210	
13.		Lithognathus lithognathus	4	4		_	
14.		Rhabdosargus holubi	4	4	7	9	
15.		Sarpa salpa	-	_	6	8	
16.	Mullidae	Pseudupeneus pleurotaenia	-	_	2	2	
17.	Pomacentridae	Abudefduf saxatilis	_		1	1	
18.	Cheilodactylidae	Chirodactylus brachydactylus	5	4	5	8	
19.	Mugilidae	Juveniles	34	44	110	201	
20.	Labridae	Juvenile	-	1	_	_	
21.		Stethojulis interrupta	-	-	_	1	
22.		Stethojulis trilineata	4	1	_	_	
23.	Blenniidae	Blennius cornutus	_	1	1	77	
24.		Blennius cristatus	-	_	_	26	
25.		Blennius fascigula	_	1	_	1	
26.		Istiblennius edentulus	-	_	_	1	
27.		Omobranchus banditus		_	_	2	
28.	Clinidae	Blennioclinus brachycephalus	_	-	_	2	
29.		Clinus cottoides		8	1	41	
30.		Clinus superciliosus	23	24	30	45	
31.	Callionymidae	Charibarbitus celetus	-	_	_	4	
32.	Gobiidae	Cafrogobius caffer	1	4	6	23	
33.		Gobius saldanha	2	3	3	17	
34.		Quisquilius cinctus	_	1	_	_	
35.	Soleidae	– – – Heteromycteris capensis	-	_	_	1	
36.		Synaptura marginata	_	1	-	_	
37.	Tetraodontidae	Amblyrhyncotes honckenii	2	2	-	-	

Table 3 Visual estimates and actual numbers of fish observed and subsequently collected

congrid eels, soleids and some serranids, labrids, blenniids, clinids and gobiids.

Non-secretive, cryptic species — fish which are not affected by the presence of divers but are nevertheless difficult to count on account of their cryptic colouration and/or behaviour. Between 14 and 66,7% ($\bar{x} = 32,6\%$) of the actual number were counted, exemplified in this study by ariids and some serranids, clinids and gobiids.

Schooling species — fish forming dense schools in open water which makes them difficult to count accurately. Estimated numbers varied between 55 and 100% ($\bar{x} =$ 57,4%) of those collected. Only three species were involved, *Diplodus sargus* and *Sarpa salpa* (often in mixed aggregations), and the mugilid juveniles.

Social species — fish which occur either singly or in small

groups of 5-6 individuals in the water column and which are relatively easy to count. These were generally counted most accurately (57-117%; $\bar{x} = 89,5\%$) and examples in this study were kuhliids, pomadasyids, some sparids, mullids, pomacentrids, cheilodactylids and tetraodontids.

The correction factors were estimated for each of these four groups (Table 4). Clinus superciliosus was placed with the social species for this study in spite of being a non-secretive, cryptically-coloured fish. This was on account of its habit of approaching and investigating divers which nullified the effects of its cryptic colours on counting accuracy. More specimens of Diplodus cervinus, D. sargus, Chirodactylus brachydactylus and Stethojulis trilineata were counted than were collected (Table 3). The missing specimen of C. brachydactylus was observed wedged in a crevice but could not be dislodged and the



Fig. 2 The accuracy of visual estimates, calculated as the percentage of the number of each species collected that was visually counted. The numbers at the base of each histogram refer to the fish species listed in Table 3. A. Secretive species, B. Non-secretive, cryptically-coloured species, C. Schooling species, D. Social species.

Table 4 The mean percentage accuracy (\bar{x}) of the visual censuses of, and correction factors (*Cf*) calculated for, the four classes of fish defined in the text

Fish Group	x	Cf
Secretive	0,16	615,35
Non-secretive, cryptic	32,63	3,06
Schooling	57,36	1,74
Social	89,47	1,12

species was therefore dealt with as though it had been counted with 100% accuracy. It is possible that a single specimen of D. cervinus was overlooked but it was nevertheless treated as having been overestimated when the factor was calculated. The other two species were disregarded for the purpose of determining the correction factor. The reasons were that the small size (10-15 mm)SL) and transparency of D. sargus in this case, combined with poor visibility in the pool after the poison had been laid is likely to have resulted in specimens having been overlooked and that S. trilineata, although cryptically coloured, has a particularly noticeable swimming action and all four specimens were observed together at one time by both divers. It therefore seems probable that the uncollected examples dived in typical labrid fashion into the sand when under stress from the poison and died there. The mugilid juveniles from Pool 1 were also disregarded when calculating the correction factors as specimens were observed to enter the pool with an untimely large wave, died rapidly and were then scooped up and inadvertently mixed with those previously collected, with a resultant bias.

One marked feature of the data on the accuracy of visual censuses is that the estimates from Pool 2 are generally less accurate than those from Pool 1 (Figure 2). This is unexpected as the visibility was poorer in the latter (Table 1). In the case of the schooling types, it is not possible to evaluate this feature as both species in Pool 1 had to be disregarded for the reasons discussed above. One possible explanation for the decrease in accuracy with the other species in Pool 2 could be the presence of thicker algal cover combined with greater visibility giving these species the opportunity to observe the divers from a greater distance. This would allow them greater time to hide. Alternatively, it could purely be a factor of thicker cover. Thus, the weed-dwelling Clinus superciliosus was censused more inaccurately in Pool 2. This may be related to the denser algal cover acting synergistically with its cryptic colouration as the species is normally simple to count on account of its habit of investigating divers. The results thus reinforce the need for either a few censuses in a single habitat type or for many throughout the area in order to overcome such biases. The latter method may be slightly more inaccurate but is probably the most feasible in practice.

Test of predictive power

Estimated densities and correction factors were tested for accuracy on 24 May 1977 (Table 5). The delay of four months was necessary as it appears that it takes that long for complete recovery of fish populations from the time of application of 'pronoxfish' (Bussing 1972; Smith 1973).

The types and numbers of species expected to be present were obtained from the visual census data obtained between October 1976 and January 1977 (Table 2). Only those species which were classified as residents were in-

Family	Species	Expected number (Mean ± 2 <i>SE</i>)	Visual census (number)	Correction factor (<i>Cf</i>)	Corrected number	Actual number (poisoned)	% Error
Atherinidae	Hepsetia breviceps	8,2 - 1,2	2	1,37	3	11	-73
Serranidae	Acanthistius sebastoides	_	-	_	_	5	
	Epinephelus guaza	_	1	3,06	3	2	+ 50
Kuhliidae	Kuhlia taeniurus	-	3	1,12	3	7	- 57
Sparidae	Diplodus cervinus	$8,2 \pm 1,2$	9	1,12	10	11	- 9
	Diplodus sargus	399 ± 227	120	1,74	209	233	- 10
	Rhabdosargus holubi	$5,2 \pm 2,7$	_	_	-	_	-
	Sarpa salpa	_	36	1,74	63	67	- 6
Pomacentridae	Abudefduf saxatilis	_	-	-	_	1	
Cheilodactylidae	Chirodactylus brachydactylus	$5,2 \pm 1,5$	_	-	_	_	-
Mugilidae	Juveniles	_	5	1,12	6	6	0
Clinidae	Clinus cottoides	-	-	_	-	2	
	Clinus superciliosus	$13,4 \pm 5,9$	2	1,12	2	3	-33
Gobiidae	Gobius saldanha	$2,4 \pm 0,5$	1	1,12	1	5	- 80

Table 5 Numbers of fish expected in Pool 1, estimated from Table 2, and the accuracy of a corrected visual census when compared with subsequent poison collection

cluded as it is less likely that visitors would be encountered and even if they were, the variability in numbers is such that reasonable predictions could not be made. These results were compared with the observed values (Table 5). Sarpa salpa was not estimated although it was expected, as juveniles occur in the intertidal from May until November (Christensen 1978). Thus, expected numbers could not be calculated from Table 2 as some of those censuses were taken in December/January when the species does not occur, with a resultant distortion in the estimated densities. Hepsetia breviceps, Acanthistius sebastoides, Kuhlia taeniurus and Abudefduf saxatilis are also all seasonal residents and it was thus not possible to predict their presence/absence either. This seasonal occurrence of juveniles also explains the absence of the expected Rhabdosargus holubi (Christensen 1978) and Chirodactylus brachydactylus (Butler 1976). Similarly, Clinus cottoides could not be predicted from the data in Table 2, although it was collected in the poison collection taken from Pool 1 in January. Epinephelus guaza and the mugilid juveniles are visitors and were therefore not estimated.

The range in expected numbers of all other species was remarkably similar to those observed, with the exception of *Clinus superciliosus*. This species also occurs infratidally (Penrith 1970), and it may therefore be that it moves there in early winter for breeding purposes as the juveniles are observed later on in November/December (Christensen 1978). Another possible explanation is that the high degree of territoriality exhibited by this clinid (Massey 1976) decreases the speed of recolonization of denuded habitats.

The visual census data were corrected and then compared with the actual numbers observed (Table 5). This shows that the correction factor is surprisingly accurate with the exception of *Hepsetia breviceps*, *Kuhlia taeniurus* and *Gobius saldanha*. It is difficult to explain why the latter species was not observed accurately, but little is known of its habits and behaviour. The other two were in a mixed school with the juvenile *Diplodus sargus*, and therefore difficult to count.

Discussion

The accuracy of visual estimates has been questioned by several authors (Holmes *et al.* 1968; Smith & Tyler 1973). As Smith & Tyler (1972: 130) noted: 'Both methods of population estimate tend to give underestimates — (poison) collecting because of specimens lost or missed, visual counts because most investigators tend to undercount and miss individuals while recording data.'

Problems inherent in visual estimation techniques can be subjected to a quantitative evaluation when applied to fish in tidal pools, since the total population within the census area (assuming it is a closed system) can be sampled easily and effectively. Once the errors have been quantified, corrections can be calculated for subsequent use. In the case of secretive fish, which are missed totally (Figure 2), poisoning or other collection methods would be necessary. The correction factor described here is of value in the case of other fish groups but would need to be determined after a large number of censuses had been taken to overcome the effects of some of the errors mentioned. Once calculated, it would seem only to apply to that species or group of fish in that habitat and then only when censused by the same divers as did the original estimates. There is some evidence, however, to suggest that a correction factor is applicable to a particular diver, at least in the case of schooling and social species, rather than to a certain fish type. Thus, the factor was accurate when applied to other species and assemblages of fish of similar, known habits from the littoral zone in northern Zululand. This, though, will have to be tested further.

It would be useful to be able to obtain the correction factor without having to poison an area as errors other than those involved in estimation are included. One possible way to achieve this would be for a helper to introduce a known number of a certain species into a pool after a diver has checked to make sure that none were present beforehand. Divers to be tested could then make visual estimates with subsequent comparisons of actual and observed numbers in order to quantify each particular observer's error. This particular method would only be feasible with those species that school or occur in small groups in the water column, but not with cryptic types as there is at present no non-consumptive, simple technique with which to ensure there are none of that particular species present initially. For these fish, poison stations have to be taken in order to determine correction factors, if indeed they are valid. With the application of modern techniques, however, it may soon be possible to simulate reefs, pools or other marine habitats in giant aquaria. These could be stocked with known numbers of any fish type and valid correction factors calculated.

These results may have particular bearing on the use of visual censuses in the management of reef fish stocks, as envisaged by Brock (1954), and in broad ecological studies of fish interrelationships, as reported by Smith & Tyler (1972) and Hobson (1974). Their particular value lies in the fact that they are non-consumptive, an increasingly desirable objective in modern ecological research.

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