



# The impact of the 1998 coral mortality on reef fish communities in the Seychelles

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## Abstract

Coral reef fish communities in the Seychelles are highly diverse and remain less affected by the direct impacts of human activities than those on many other coral reefs in the Indian Ocean. These factors make them highly suitable for a detailed survey of the impacts of the 1998 mass coral mortality, which devastated the coral faunas of the region. Using underwater visual census (UVC) techniques, fish communities were sampled in three localities in the southern Seychelles and one locality in the northern (granitic) Seychelles. Initial surveys were undertaken from the latter site in 1997. Surveys were undertaken at all sites during the coral bleaching episode in 1998 prior to any major changes in the reef fish communities. Repeat surveys were undertaken in 1999 one year after the coral mortality. Over 250 fish species were sampled from 35 families. Results suggest that changes in the overall fish community structures are not great, despite massive changes in the benthic cover. Significant changes have been observed in a number of individual species. These include those most heavily dependent on live coral cover for shelter or sustenance. Future potential changes are discussed, and potential management interventions are considered. © 2002 Elsevier Science Ltd. All rights reserved.

## 1. Introduction

In 1998 a global coral bleaching event was observed which was the most geographically extensive and, for many areas, the most destructive on record (Hoegh-Guldberg, 1999; International Society for Reef Studies, 1998). Among the most severely impacted reefs were the non-continental reefs of the Indian Ocean, with mass mortalities of reef-building corals reaching 80–90% for entire reef ecosystems and nations (Wilkinson et al., 1999; Lindén and Sporrang, 1999; Sheppard, 1999). The immediate cause of this event was a warm-water episode which has been linked to the 1997–1998 El Niño Southern Oscillation, which raised surface temperatures over wide areas of the region (Wilkinson et al., 1999; Spencer et al., 2000). It seems increasingly likely, however, that the severity of this event was further exacerbated by the background increases in sea surface temperatures which have been recorded from across the region and elsewhere,

which have been linked to global climate change (Hoegh-Guldberg, 1999; Wilkinson et al., 1999).

The mortalities recorded were not restricted to reef-building corals, although these have been the most accurately measured. There was also widespread loss of soft corals and anemones (Spalding, pers. obs.). Algal growth rapidly colonises the bare surfaces left by the loss of these organisms, typically within days of a bleaching-induced mortality. Mortalities of this scale are largely unprecedented, with the exception of a mass-mortality event in the eastern Pacific associated with the 1982–1983 El Niño event (Glynn, 1991; Glynn et al., 1988). Although this earlier event covered a very large geographic area (including Costa Rica, Panama and the Galápagos Archipelago) and led to coral mortalities of 51–97%, the reefs in this region are not directly comparable, being generally small structures, or simple coral communities. The authors are unaware of any studies associated with the reef fish communities in response to this event.

Elsewhere, mass mortalities of corals have been observed over slightly smaller areas from other causes, and are also useful for developing a wider understanding of the processes involved. In the Caribbean, many reefs

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have lost a large proportion of their live coral cover since the 1980s, typically linked to a complex sequence of events, including the die-off of the algal-grazing sea urchin *Diadema antillarum* widespread impacts of coral diseases, and other factors including overfishing, pollution and hurricane damage (Hughes, 1994; Spalding et al., 2001). In the Indo-Pacific the mass-infestations of the crown-of-thorns starfish *Acanthaster planci* which have been recorded since the 1960s provide a more directly comparable form of change (Hart et al., 1996; Kenchington and Kelleher, 1992; Sano et al., 1987; Sapp, 1999; Williams, 1986), being both rapid and substantial. However even in these *Acanthaster* events, the spatial extent of the damage is not comparable to the 1998 coral reef bleaching event in the Indian Ocean.

Such changes are likely to have an impact on the mobile fauna of the coral reef, and this paper examines the nature of such changes for reef fish communities.

The factors influencing the community structures of reef fish are still a matter of considerable debate. A number of authors have stressed the importance of recruitment supply and hence survivorship during larval phases. Other models have placed more weight on the importance of post-settlement influences, including direct competition for resources (both food and shelter), predation and disturbance (Jones, 1991). It seems likely that all of these factors may have a role to play, and that their relative importance may vary between species, trophic levels and localities (Roberts, 1996). They may also act at different intensities as external factors are varied.

In the present study, the loss of live coral cover equates to a large change of habitat, coral cover being reduced from being the dominant living surface cover to a minor element in an algal dominated ecosystem. Immediate changes might be expected among those species whose populations are resource limited, either by algae or coral abundance. Subsequent effects might follow, with changes in piscivores and invertebrate feeders following changes in their prey populations. Such predictions have been validated in a small number of studies.

Williams (1986) looked at the changes to a broad range of fishes (146 species) on three reefs 6–10 months after the impact of an *Acanthaster* outbreak. This outbreak reduced live coral cover by 55–90%, however nearby reefs were unaffected. For the most part it was difficult in this study to distinguish the impacts of the coral die-off from the naturally high spatial and temporal variability in these communities. The major exception to this was a clearly defined fall in abundance in a number of corallivorous Chaetodontids. The same study also looked at recruitment in a number of species before and after *Acanthaster* infestation and did notice a disproportionate decline in abundance of recruits in 17 species, most of which have a close association with live coral at the time of larval settlement (e.g. certain *Chomis* and *Chaetodon* species).

Massive algal increases in the Caribbean following *Diadema* mortality, although not directly linked to coral mortalities, were shown to produce significant increases in herbivorous fish numbers (Carpenter, 1990; Robertson, 1991).

More recently, Lindahl et al. (2001) have published a study of the impacts of the 1998 bleaching event on the coral reef fishes on a number of shallow transplanted coral plots in Tanzania. Their study, 6 months after the event, showed an overall increase in fish abundance, largely linked to an increase in herbivores.

Sano et al. (1987) provide a longer term perspective of the impacts of an *Acanthaster* outbreak, again providing a broad-scale community perspective. In this study the coral death was followed by significant erosion of the former reef area to a rubble plain of low structural complexity. Their study shows that the transformation from live reef to dead reef to rubble reef was associated with decreases in diversity and abundance and the total loss of corallivores during this time. Even herbivores and benthic-animal feeders were affected, although these impacts were less clear on the dead reef than the rubble reef. They suggest that many of these changes can be related to changes in structural complexity and that decreases in food availability may only be of minor significance.

Changes in abundance are a direct and easily observed impact, however the changes induced by the 1998 bleaching could act in a number of more subtle ways, perhaps increasing or reducing fecundity or growth-rates in particular groups or altering competitive ability. The impacts of such changes may take longer to appear in the community structures and will be further influenced by future changes to the benthic substrate cover and surface complexity.

## 2. Methods

### 2.1. Study sites

The Seychelles incorporates numerous islands and coral reefs scattered over a large area of the western Indian Ocean. The greatest concentration of islands, and the majority of the human population, are found in the north of the country where there is a series of high islands of continental origin, known as the granitic Seychelles. The remaining islands are all carbonate structures and include atoll and platform structures, both at sea level and at slightly raised elevations. Population densities are low, particularly in the southern islands, and the human pressures on the coral reef resources must be regarded as relatively low. There is no major export market for reef fish and local consumption is not high. Other threats to coral reefs centre on more localised developments, notably the extensive land rec-

lamation which has destroyed what was once the most extensive fringing reef system in the islands, on the main island of Mahé. Elsewhere there are localised problems of pollution, while tourism development is having some impact on the more remote southern islands. Away from these areas, there remain large areas of coral reef which are relatively unimpacted, and on which fishing pressures are still relatively low. For this particular study, four sites were utilised, one in the granitic Seychelles and three in the southern Seychelles.

*Cousine Island* is a small island close to Praslin, and is run as a private nature reserve. Offshore it has a highly varied series of communities, including: fringing reef, submerged and intertidal rocky-reef communities on granitic substrates, macroalgae dominated communities, compacted rubble slopes and bare sandy slopes. The best developed coral reef community, and the site for the present study, is a fringing structure which runs for several 100 m along the north-east shore. Although a sub-surface structure, lacking a clearly defined reef flat or reef crest there is a reef slope which descends from a depth of 2–3 m down to a depth of 10 m where it meets a level sandy plain with macro-algae and occasional coral heads. Although there is some fishing in this area, levels are low. The strict protection afforded to the terrestrial environment makes it unlikely that there are any serious terrestrial stresses acting on the marine communities.

*Alphonse Atoll* is located at the southern end of the Amirantes ridge about 450 km south of the granitic Seychelles. There is a single island at the northern end, and a wide reef flat enclosing the generally shallow (< 10 m) lagoon, with only a single shallow channel in the south. There is a low-relief spur and groove development descending from the reef flat, and a 50–150 m wide fore-reef slope descending to about 15–20 m before a steep drop-off. A single study-site was selected on the western side of the atoll.

*St Pierre Island* is a small raised carbonate platform reaching about 5 m above present sea levels. It is some 250 km south of Alphonse and over 600 km south of Mahé. There are reefs on all sides of the island, although fully developed reef structures have not developed and there is no reef flat or reef crest. The north-west coast is characterised by a gently sloping profile for 100–200 m, dominated by high coral cover, as at Alphonse there is a sharp change at 15–20 m with a steep drop-off. The opposite, south-eastern, side of the island is quite different, with a shallow slope profile up to 2 km offshore, and generally lower coral cover above 10 m depth. Two sites were selected at St Pierre representing these two sides of the island.

At each of these broad locations, individual sites were selected on reef slopes away from unusual features such as lagoon channels or the edges of reefs next to non-reef communities. On particular dives the location of the first census was broadly pre-selected from a map or chart,

but to avoid fine-scale bias, the census was undertaken immediately below the point of entry into the water, before the reef was seen by the diver. Subsequent censuses on the same dive were placed using a pre-determined random number of fin-strokes away from the initial count.

Data were gathered on three consecutive years from the study-site in Cousine, in February 1997, May 1998, and March 1999. Data were gathered from the southern Seychelles sites in April 1998 and March 1999.

## 2.2. Field methods

Reliable quantitative data covering a broad range of species was gathered utilising a fixed point visual census technique (Bohnsack and Bannerot, 1986; Roberts and Polunin, 1992). Further details of this method are given elsewhere (Spalding, 1999). At each locality six independent samples were taken and these results amalgamated for the subsequent analyses. Each sample consisted of a 20 min count of reef fish in a 10 m diameter area of reef and the overlying water column. Counts were undertaken at 15 m depth on the oceanic reefs of St Pierre and Alphonse, and at 8–10 m depth on the fringing reefs of Cousine. The majority of fish found, representing over 30 families on the reef, were sampled (certain cryptic, nocturnal or rare groups were ignored), and 40–60 species were typically seen per count. Observed species were marked onto pre-prepared sheets: roving pelagics were counted immediately and thereafter whenever a new individual or group passed through the count area. Site-associated benthic species were counted on a species by species basis throughout the count. After approximately 10 min, the diver moved away from a central position for the census and slowly circled the sample site, noting additional individuals or species not visible from the central location.

One of the general sampling problems for coral reef fish is the large number of relatively rare species. Although the described method allows for detection of large numbers of species, sample sizes are small. Transect and plotless transect methods can provide a more reliable approach for the sampling of certain species as they can cover wider areas, however they do not allow for the accurate assessment of abundance for a large number of species. For those species whose sample sizes are small it is usually possible to highlight trends, or to amalgamate on ecological grounds to establish more general patterns.

On each count a number of additional notes and comments were taken. These included a semi-quantitative assessment of benthic cover: summarising percentage cover into 12 categories of substrate. The aspect and angle of the reef slope were also noted, together with an assessment of the reef surface complexity based on a 10-point scale.

2.3. Data analysis

Benthic cover data were averaged for each site and presented to provide a basic understanding of the underlying changes. Summary plots of the changes in reef fishes by trophic group were prepared. While such plots point to some overall trends they also mask important details. The highly specific niche and dietary requirements of many reef fish points to the need for analysis at the level of individual species.

The problem of low abundance and large numbers of zero counts at the species level, reduces the utility of many commonly used parametric tests. A sub-group of more abundant or better-sampled species was prepared.

Any species with a record of more than 15 individuals spread over 50% of the censuses (i.e. over three or more counts, to avoid rare schooling species) in at least one site in any year were selected for further analysis. Individual counts were tested to determine whether they were sampled from a randomly distributed population of fish, and hence conformed to a Poisson distribution. This was carried out by a goodness of fit test using the *G* statistic, derived from a log-likelihood ratio (Zar, 1996). Those species whose distributions were not significantly different from a Poisson distribution using this test were subjected to the following analyses.

The data from both sampling periods were modelled as a single Poisson distribution with mean and variance

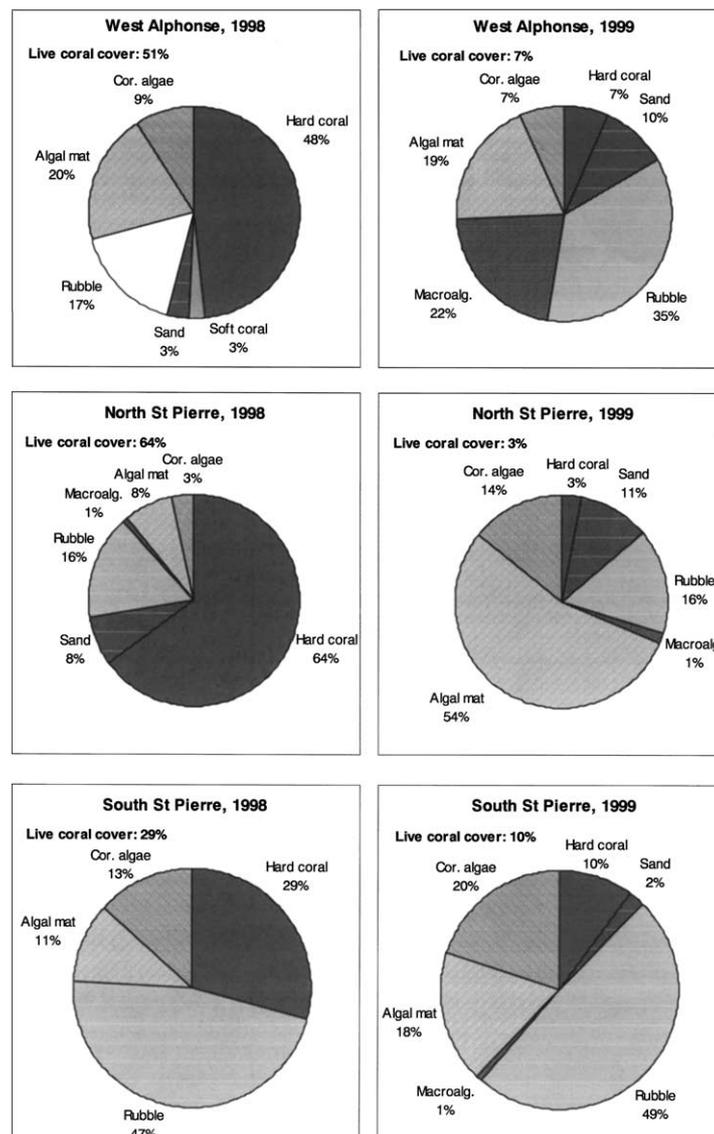


Fig. 1. Changes in the benthic substrate cover between 1998 and 1999 at three locations in the Southern Seychelles. Figures are based on rough visual estimates taken following fish counts. The difference between algal mat and rubble is to some degree blurred as most rubble has an algal covering. The most important difference to note is the combined loss of hard and soft coral, indicated in text above each figure. These dramatic declines of living coral cover are likely to be underestimates as some coral death had already occurred prior to the survey work.

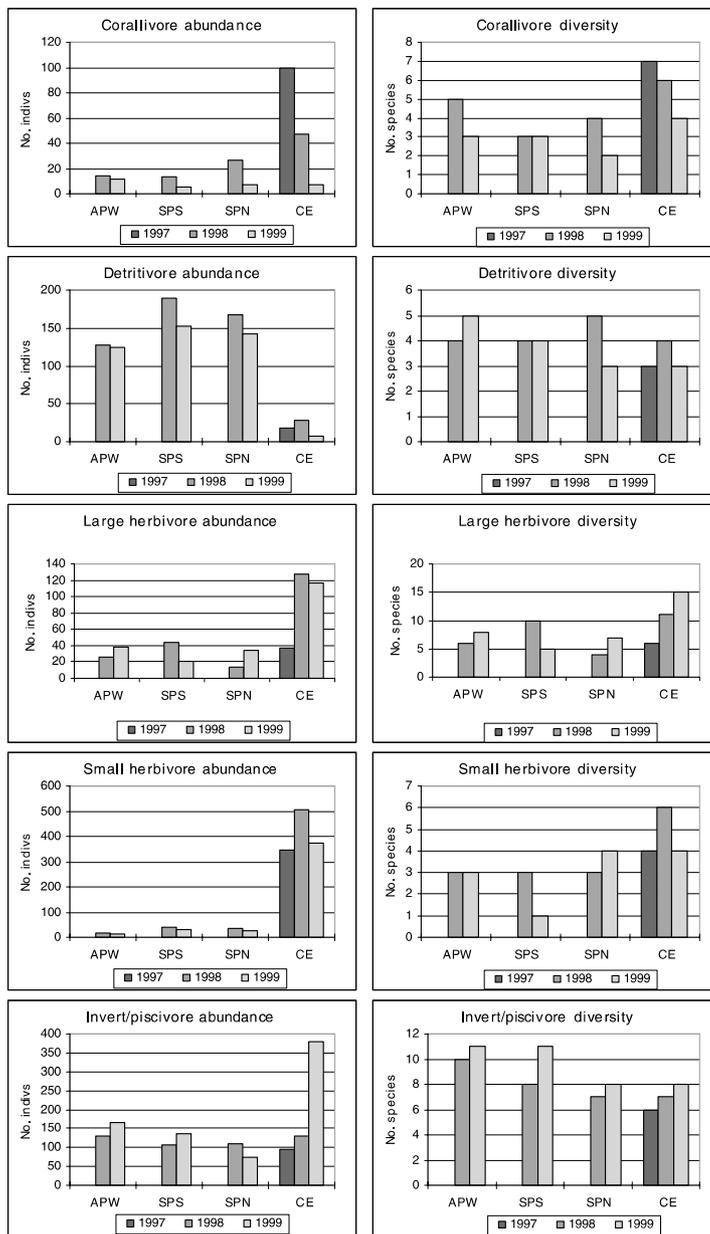
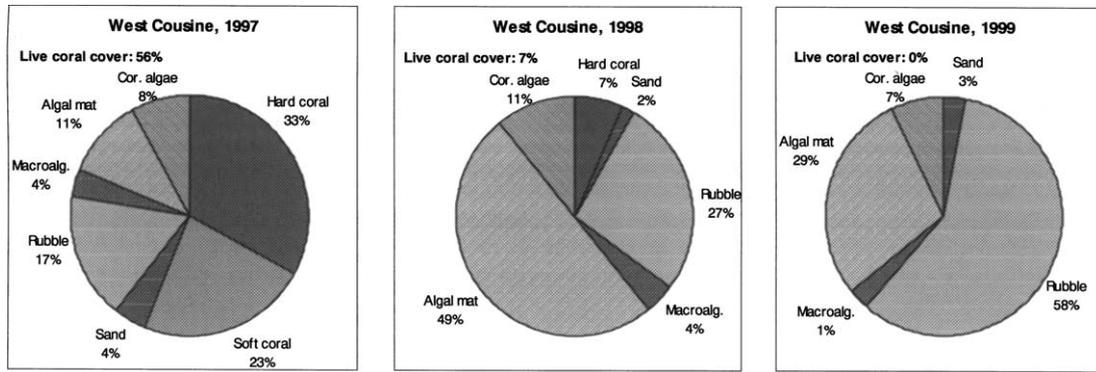


Fig. 2. Changes in the benthic substrate cover over three years at Cousine Island. Notes as for Fig. 1, however it is also important to note that this was the last site to be sampled in 1998, some 4 weeks after the previous sites and hence the coral mortality was already well advanced when these estimates were made.

$\mu_0$  (where  $\mu_0$  equals the mean of all the data). This model constituted the null hypothesis ( $H_0$ ) that the fish populations were identical during the two sampling periods. The alternative hypothesis ( $H_A$ ), that the fish populations were different, was then modelled as two distinct Poisson distributions, one for each counting period, with mean values  $\mu_1$  and  $\mu_2$  (where  $\mu_1$  equals the mean of the data from the first year, and  $\mu_2$  equals the mean from the second). The maximum likelihood for each of these models was calculated and a likelihood ratio test performed (see Appendix A for a more detailed description of this test). The likelihood ratio value was then compared against a  $\chi^2$  distribution with one degree of freedom and a probability obtained, where  $P < 0.05$  the null hypothesis ( $H_0$ ) was rejected and  $H_1$  accepted.

### 3. Results

Details of the coral bleaching event have been described elsewhere (Spencer et al., 2000). Figs. 1 and 2

show the semi-quantitative substrate data gathered from the study-sites themselves. While based on simple visual estimates, the extent of the changes to the substrate at these locations is clearly shown. Coral mortality is likely to be underestimated in these figures as some mortality had already occurred at the time of the 1998 survey and hence “original” coral cover was probably much higher than indicated.

A summary of the changes in the fish communities at the level of trophic groups is provided in Fig. 3, plotting changes in both abundance and diversity of species. Eight broad trophic groups were identified, with the herbivorous group further sub-divided into large and small species (“large” species defined as those with total length of adults over 30 cm). From these figures a number of patterns can be seen, notably small declines in abundance and diversity of corallivores in all sites. There are also notable differences between patterns in the three southern Seychelles sites and the site in the granitic islands. The significant ecological differences between these two regions are considered elsewhere

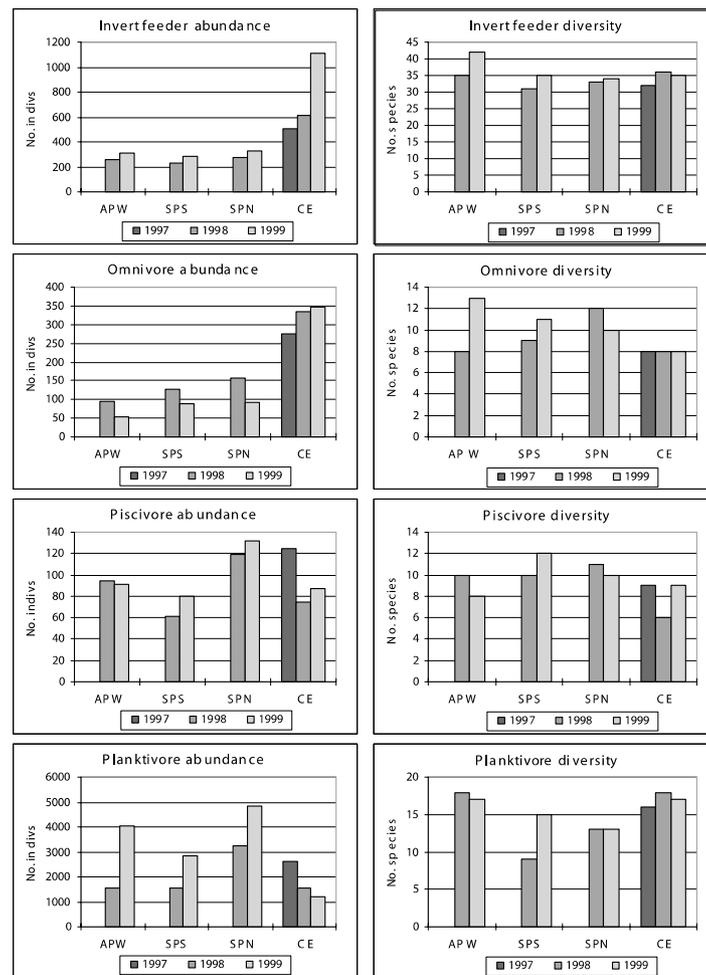


Fig. 3. Changes in abundance and diversity of different trophic groups at the four study sites between 1997 and 1999. APW – Alphonse West; SPS – St Pierre South; SPN – St Pierre North; CE – Cousine East.

(Spalding, in press), but these differences show the need for independent analysis of trends in the two areas.

A more detailed analysis of the population changes for individual species data was undertaken for the sub-group using the methods described. Fig. 4 illustrates the general approach underlying such tests for two samples.

For the southern Seychelles sites, some 42 fell into the sub-group of better-sampled species, and the count totals for each are presented in Table 1. Of these datasets, 28 conformed to a Poisson distribution and were analysed using the likelihood ratio test, comparing the individual count data on the two consecutive years. The *P* values in Table 1 show the significance of the difference between these distributions on consecutive years.

A number of species in this table appear to show significant changes. Of particular interest are those species which show a consistent trend at all sites, especially when significant in more than one site. Only one species, *Plectroglyphidodon johnstonianus*, showed a consistent and significant decline at all sites. This small species is highly dependent on live coral for shelter. Whilst a number of the planktivore species showed increases at all three localities (see also Fig. 3), the schooling nature of most of these species means that more detailed analyses of these changes are not possible with the present samples.

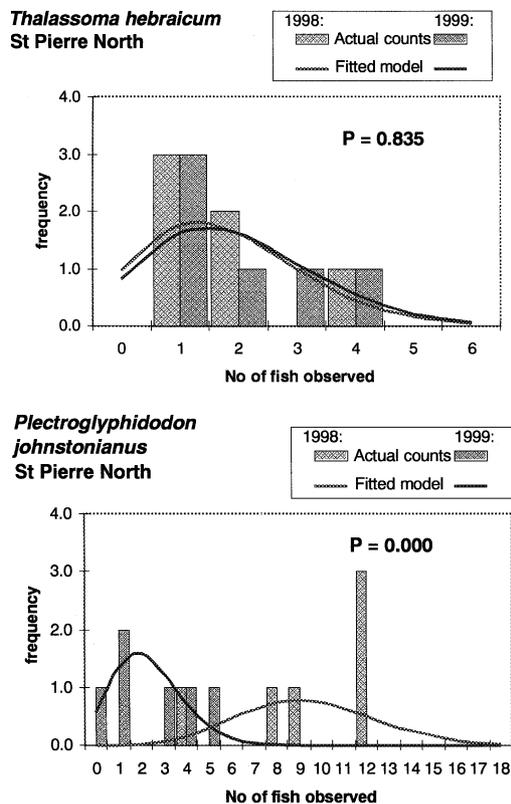


Fig. 4. Examples of data from two species, one showing a significant change, the other not. The bars show the actual data, while the curves show the fitted Poisson distribution. The LR test evaluates the similarity of the two distributions.

A similar series of tests were undertaken in the northern granitics. A subset of 44 species was selected of which 21 conformed to the Poisson distributions, and these were analysed using the likelihood ratio test. Although data were available for three years, pairwise tests were still performed in order to capture all possible trends. Three comparisons were thus undertaken for each species, comparing 1997 with 1998, 1997 with 1999 and 1998 with 1999. The findings are presented in Table 2.

A large number of species shown in this table appear to show significant changes. Where these trends are continued over all years they are of particular interest. The two corallivorous species tested both showed significant declines in all comparisons. In contrast to the sites in the Southern Seychelles several of the planktivorous species also showed reductions, although again the problem of schooling presents further analysis of these results.

#### 4. Discussion

The findings show complex and multi-directional changes in reef fish assemblages associated with the mass mortality of corals in 1998. Most of the changes can only be clearly observed at the level of individual species. A number of specific observations can be highlighted:

- There were notable decreases in corallivores, notably Chaetodontids, but also *Oxymonacanthus longirostris*. The percentage decline in these species did not equal that of the decline in coral cover, however it is conceivable that there may be some lag in the response and that these populations may still have been declining overall.
- There was a decline in the *Plectroglyphidodon johnstonianus*. At the depth of the surveys this is one of the most dominant small damselfish which hide amongst the branches of live coral. It seems likely that in shallower waters other similar “coral nestlers” may have declined in abundance.
- There were increases in several invertebrate feeders.
- A number of other minor changes appear to contrast between high island fringing reefs and oceanic islands.

Overall, however, there was marked stability at the level of trophic groups and individual species. Even where apparently significant results are observed, considerable caution must be applied. Given the large number of pairwise comparisons which have been undertaken, there is a risk of Type 1 errors and of over-estimating the number of significant results. Furthermore, it has not been possible with the present work, to investigate the natural temporal variability in fish

Table 1  
Count totals by site and year for the more abundant and evenly distributed species in the Southern Seychelles

Species	Trophic group	APW 98	APW 99	<i>P</i>	SPS 98	SPS 99	<i>P</i>	SPN 98	SPN 99	<i>P</i>
<i>Chaetodon meyeri</i>	co	8	9	0.808	7	2	0.410	15	6	<b>0.046</b>
<i>Centropyge acanthops</i>	dt	11	23	0.037	33	41		24	16	0.204
<i>Centropyge multispinnis</i>	dt	59	34	<b>0.009</b>	45	49	0.680	64	47	0.106
<i>Ctenochaetus striatus</i>	dt	13	20	0.221	20	0		3	0	
<i>Ctenochaetus strigosus</i>	dt	45	40		92	60	<b>0.009</b>	76	79	
<i>Acanthurus leucosternon</i>	hb	11	4	0.065	35	29	0.453	5	6	0.763
<i>Naso lituratus</i>	hb	2	6	0.148	0	0		10	17	0.175
<i>Plectroglyphidodon lacrymatus</i>	hb	0	0		1	0		22	3	<b>0.000</b>
<i>Scarus tricolor</i>	hb	4	7	0.363	6	6	1.000	8	21	
<i>Cephalopholis nigripinnis</i>	ip	29	32	0.701	46	45	0.917	45	30	0.082
<i>Cirrhilabrus oxycephalus</i>	ip	12	27	0.015	2	10	0.016	5	1	
<i>Lutjanus gibbus</i>	ip	8	49		0	8		0	0	
<i>Paracirrhites arcatus</i>	ip	36	28		26	31	0.508	17	21	0.516
<i>Paracirrhites forsteri</i>	ip	29	20	0.197	25	12	<b>0.031</b>	31	10	<b>0.001</b>
<i>Gomphosus caeruleus</i>	iv	19	17		15	15	1.000	18	21	
<i>Halichoeres cosmetus</i>	iv	11	18	0.191	16	18		8	20	0.021
<i>Labroides bicolor</i>	iv	10	9	0.819	8	7	0.796	18	15	
<i>Labroides dimidiatus</i>	iv	19	26		8	22		32	36	0.628
<i>Parupeneus macronema</i>	iv	5	15	0.022	10	4	0.103	7	4	0.363
<i>Pseudocheilinus hexataenia</i>	iv	26	31	0.508	42	56	0.157	48	39	0.334
<i>Pseudocheilinus octotaenia</i>	iv	1	7		15	22	0.248	20	25	
<i>Thalassoma hebraicum</i>	iv	17	21	0.516	15	12	0.563	11	12	0.835
<i>Plectroglyphidodon johnstonianus</i>	om	55	14	<b>0.000</b>	92	57	<b>0.004</b>	57	14	<b>0.000</b>
<i>Zebrasoma scopas</i>	om	9	3		19	3		50	51	0.921
<i>Caranx melampygus</i>	pi	31	48		6	27	0.000	50	10	<b>0.000</b>
<i>Cephalopholis miniata</i>	pi	22	11	0.053	10	15	0.316	41	41	1.000
<i>Epinephelus fasciatus</i>	pi	7	8	0.796	17	2		0	0	
<i>Lutjanus bohar</i>	pi	23	12	0.061	4	9	0.160	3	5	0.477
<i>Acanthurus thomsoni</i>	pk	9	1		2	25		195	145	
<i>Caesio teres</i>	pk	0	0		100	203		295	90	
<i>Chromis dimidiata</i>	pk	531	440		200	375		470	725	
<i>Chromis ternatensis</i>	pk	247	83		324	380		237	125	
<i>Chromis weberi</i>	pk	30	63		0	0		0	0	
<i>Cirrhilabrus exquisitus</i>	pk	3	115		0	60		7	0	
<i>Hemitaenichthys zoster</i>	pk	2	0		0	25		7	52	
<i>Lepidozygus tapienosoma</i>	pk	136	745		198	112		389	800	
<i>Melichthys indicus</i>	pk	9	5		10	17		13	12	0.841
<i>Nemanthias carberryi</i>	pk	476	2195		692	1160		1361	2250	
<i>Nemateleotris magnifica</i>	pk	0	13		0	22		0	0	
<i>Odonus niger</i>	pk	10	66		0	0		0	0	
<i>Pseudanthias squamipinnis</i>	pk	102	285		2	42		97	510	
<i>Pterocaesio tile</i>	pk	0	0		7	435		110	95	

The results of statistical analysis using the likelihood ratio test, comparing individual count records for the two years, are presented in the third column for each site, where no *P* value is recorded, this is because the data did not conform to a Poisson distribution, making the analysis inappropriate. Species are sorted into trophic groups. All significant results ( $P < 0.05$ ) are marked in bold. Non-italicised are those with a significant decrease, while italicised showed a significant increase. APW – Alphonse West; SPS – St Pierre South; SPN – St Pierre North.

communities, as all sites were heavily impacted. It seems likely that some species do show considerable natural variability (Williams, 1986), and some illustration of this may be interpreted from the significant changes observed in Table 2 which actually show opposing directions of change between 1997–1998 and 1998–1999. Where apparently significant changes can be clearly associated with the observed changes to the benthic cover, as with the declines in corallivores and coral nestlers, we can be more confident that the changes can indeed be related to the 1998 coral mortality.

A number of further points must be made. This work was based on observations made in 1999. At this point in time there had been relatively little structural changes to the reef surface topography. (Estimates of reef surface complexity taken in association with each census showed no trends in the southern Seychelles, and only a small, non-significant decline over 3 years in the granitic Seychelles.) There were also very few signs of recovery. It seems highly likely that the processes of change in the fish communities will continue over a considerable time period, associated with continuing changes to the ben-

Table 2  
Count totals by year for the more abundant and evenly distributed species in the granitic Seychelles

Species	Trophic group	Mean per count 97	Mean per count 98	Mean per count 99	97–98	98–99	97–99
<i>Labrichthys unilineatus</i>	co	6.7	4.5	0.2	0.069	<b>0.000</b>	<b>0.000</b>
<i>Oxymonacanthus longirostris</i>	co	6.4	1.7	0.0	<b>0.000</b>	<b>0.003</b>	<b>0.000</b>
<i>Ctenochaetus striatus</i>	dt	2.3	2.8	0.3			<b>0.001</b>
<i>Scarus sordidus</i>	hb-l	1.6	3.5	4.5	0.013	0.386	0.000
<i>Siganus argenteus</i>	hb-l	1.8	11.7	1.2			
<i>Acanthurus triostegus</i>	hb-s	14.9	29.5	15.0			
<i>Naso lituratus</i>	hb-s	0.5	0.8	4.3	0.405		
<i>Plectroglyphidodon lacrymatus</i>	hb-s	41.0	41.7	41.7			
<i>Scarus spp.</i>	hb-s	1.3	11.5	1.3			0.883
<i>Epibulus insidiator</i>	ip	1.9	1.8	1.3			
<i>Lutjanus fulviflamma</i>	ip	10.8	18.3	23.2			
<i>Lutjanus gibbus</i>	ip	0.0	0.5	37.2			
<i>Anampses melagrides</i>	iv	3.4	3.2	2.5	0.783	0.492	0.290
<i>Gomphosus caeruleus</i>	iv	4.0	4.0	2.5	1.000	0.148	0.099
<i>Halichoeres hortulanus</i>	iv	2.3	1.2	1.8	0.080	0.344	0.491
<i>Labroides dimidiatus</i>	iv	5.0	7.2	4.2	0.075		
<i>Mulloidichthys flavolineatus</i>	iv	0.3	0.7	40.8	0.197		
<i>Neoniphon sammara</i>	iv	20.9	16.5	19.2			
<i>Pseudocheilinus hexataenia</i>	iv	5.7	6.0	4.7	0.782	0.317	0.381
<i>Sargocentron diadema</i>	iv	21.2	35.8	85.0			
<i>Thalassoma hebraicum</i>	iv	2.9	1.5	2.8	0.059	0.114	0.922
<i>Zanclus cornutus</i>	iv	3.2	6.0	3.5			
<i>Abudefduf vaigiensis</i>	om	0.0	0.0	6.5			
<i>Plectroglyphidodon johnstonianus</i>	om	5.8	4.0	0.0	0.115	<b>0.000</b>	<b>0.000</b>
<i>Pomacentrus sulphureus</i>	om	35.6	45.7	48.0	0.001	0.555	0.000
<i>Zebrasoma desjardini</i>	om	1.3	3.5	1.8	0.004	0.075	0.422
<i>Cheilodipterus spp.</i>	pi	11.4	7.7	4.0	<b>0.021</b>	<b>0.008</b>	<b>0.000</b>
<i>Caranx melampygus</i>	pi	0.8	0.2	3.3			
<i>Oxycheilinus digrammus</i>	pi	1.6	2.8	0.8	0.085	<b>0.009</b>	0.176
<i>Lutjanus bohar</i>	pi	1.3	0.5	4.0	0.111	0.000	0.000
<i>Abudefduf sexfasciatus</i>	pk	5.0	2.0	1.3		0.369	
<i>Chromis dimidiata</i>	pk	5.3	1.2	2.5	<b>0.000</b>	0.084	<b>0.006</b>
<i>Caesio lunaris</i>	pk	1.3	27.5	0.0			
<i>Caesio teres</i>	pk	1.7	0.0	0.2			
<i>Chromis ternatensis</i>	pk	9.3	4.2	3.0			
<i>Chromis weberi</i>	pk	5.7	0.8	1.0			
<i>Caesio caeruleaurea</i>	pk	98.4	0.2	36.7			
<i>Chromis atripectoralis/viridis</i>	pk	2.8	3.5	12.5			
<i>Cirrhilabrus exquisitus</i>	pk	7.9	5.3	1.3			
<i>Heteropriacanthus hamrur</i>	pk	16.1	1.5	0.2			
<i>Myripristis spp.</i>	pk	30.3	47.0	32.0			
<i>Pterocaesio tile</i>	pk	159.2	135.7	65.8			
<i>Pomacentrus caeruleus</i>	pk	90.7	31.0	33.5			
<i>Pterocaesio marri</i>	pk	0.0	0.0	9.7			

The results of statistical analysis using the likelihood ratio test, comparing individual count records each pair of years, are presented in the final column for each site, where no *P* value is recorded, this is because the data did not conform to a Poisson distribution, making the analysis inappropriate. Species are sorted into trophic groups. All significant tests ( $P < 0.05$ ) are marked in bold. Non-italicised are those with a significant decrease, while italicised showed a significant increase.

thic cover, but also incorporating some lag-time behind such changes. This may be particularly the case for larger and longer-lived species which are able to survive for longer periods of sub-optimal conditions, but also may also take longer to recruit and change adult populations.

The patterns emerging from this study are further supported by other studies on fish communities following non-bleaching related mortality events. As already

mentioned, Williams (1986) was unable to show significant changes in fish species other than a small group (not all) of the corallivorous Chaetodontids, despite losses of 55–90% of live coral cover on his study sites on the Great Barrier Reef. In a study focussed on roving herbivorous fishes, Hart et al. (1996) showed no clear changes in numbers or biomass as a result of *Acanthaster* impacts, although there were minor (and contradictory) responses for some individual species. The more

significant increases in abundance observed in Tanzania (Lindahl et al., 2001) are clearly of interest – it may be that the shallow depth of this study leads to increases in productivity further encouraging the increases in herbivores. This latter study also showed declines in three “coral nestlers”, damselfish which rely on live coral for shelter.

Over the longer term, changes are more likely to become significant. Wass (1987, cited in Hart et al., 1996) showed increases in densities of larger roving herbivores in American Samoa over a 7-year period following an *Acanthaster* outbreak. By contrast, Sano et al. (1987) followed the impacts of an *Acanthaster* outbreak at a site two and four years after a complete coral mortality. They showed declines in abundance and diversity in four broad trophic groups, and in both resident and visiting species. These changes were clearly linked to the structural breakdown of the reefs from a complex structure to a rubble plain and they suggest that the changes were linked both to a reduction in food availability and loss of living space or shelter.

The complexity of responses shown in the present work, and mirrored by the findings of others, is not surprising. Ecologists remain divided as to the driving forces which define community structures and patterns. Jones (1991) describes four broad models. Under the competition model, resources are fully utilised and species exist in a fairly tight equilibrium, with typically narrow and specialised niche requirements. The lottery model still follows the pattern of full resource utilisation, however species composition may be highly variable and determined by stochastic events. Under the predation disturbance model it is suggested that resources are not fully utilised, but that populations are kept in check by processes of predation and/or disturbance. Finally, the recruitment limitation model suggests that resources are not fully utilised, but rather the community structure is determined by larval supply.

It is clear that the impact of mass mortality will have considerably different effects depending on which of these models holds true, and on the more specific details of limiting resources. Roberts (1996) has suggested that elements of each of these models may apply to different components of the reef ecosystem, and indeed many of the observations described here would further support this. Thus changes in the corallivorous species would appear to support some degree of food supply limitation on these populations. By contrast the relatively slow response of herbivores to increasing algal cover could be indicative of recruitment or predation limitation.

The importance of reef surface complexity as a limiting factor on some reef fish abundances has been widely observed (Caley and St John, 1996; Friedlander and Parrish, 1998; Roberts and Ormond, 1987) and this

may be a major factor over the longer term. This remains difficult to predict. Rapid rates of bioerosion, or significant storm events could lead to a reduction in the benthic complexity and lead to significant losses as observed around Iriomote Island in Japan (Sano et al., 1987). By contrast, if the physical structure remains, there could be increases in herbivores, as already observed in Tanzania (Lindahl et al., 2001) and in American Samoa (Wass, 1987).

The spatial extent and ecological scale of the coral mortality in the western Indian Ocean in 1998 was far greater than any of the other major mortality events described to date (Spalding et al., 2001), and the impacts could continue to develop for a number of years. Rates of recruitment of new coral to the reefs may be affected by the massive reduction in overall coral populations over several thousand square kilometres. Similarly then, recovery of reef fish populations, including coral nestlers and corallivores, may be impacted by these changes. Further mass-bleaching events have been predicted and will serve to further exacerbate some of these longer-term changes. Whether the impacts of such changes can be mitigated through management interventions remains open to question. Spalding (pers. obs.) showed much higher levels of coral survivorship in a few small areas, including shallow lagoon bommies and atoll channels. It may be that these small surviving patches are critical for the re-stocking of reefs, with corals and perhaps even reef fish if conditions deteriorate. The reason why such populations survived remains open to question, however it is possible that these populations were better adapted to temperature fluctuations, in which case they may be of critical importance in providing new recruits with genetic resilience to survive in a changing climate. The identification and protection of these small surviving communities may be of considerable importance for region-wide coral reef recovery.

### Acknowledgements

The authors would like to thank the following people for their various inputs into this work: Peter Hitchin, Stella Le Maitre, Fred Keeley and all on Cousine Island; Mr John Collie and the Seychelles Marine Park Authority; Jeanne Mortimer; Clare Bradshaw, Tom Spencer, Kristian Teleki and others on research cruises, including Alve Henricson and the crew of R.V. Searcher in 1998, and Guillermo Cryns, Owen Jenkins and the crew of S.Y. Thalassi in 1999; and David Plowman. Part of the work described in this paper was undertaken as part of the Royal Geographical Society—Royal Society Shoals of Capricorn Programme, western Indian Ocean, 1998–2001. This is Shoals Contribution No. P014.

## Appendix A. A statistical analysis of fish counts using a likelihood ratio test

### A.1. Introduction

Simple parametric tests are extremely useful for the analysis of data, but require that the data conform to a normal distribution. Where this is not the case, the validity of using such tests is questionable and alternative approaches are required. A useful approach follows recognition that the mean values of samples drawn from populations of any distribution tend towards a normal distribution (Central Limit Theorem) (Dudewicz and Mishra, 1988). Analysis using parametric tests can then proceed on mean values from independent samples. It is frequently not possible to obtain sufficient data in order to do this, however, and analyses must then be performed using non-normally distributed data. Non-parametric tests are independent of assumptions of distribution and can be utilised, however the power of these analyses can be low, especially where there is limited data.

Another approach is to model the data to an appropriate alternative distribution, in order to derive parameter values which describe the data. For each parameter set, the likelihood of the actual data being derived from a population with that set can be calculated. Furthermore, a particular parameter set can be identified for which the value of this likelihood is maximised. Maximum likelihood values can then be used to make statistical inferences about how well actual data fit to specifically defined models.

A method is presented here which allows for the comparison of data sets drawn from a population of a particular distribution. For the purposes of this study, it was considered that populations of fish might be randomly distributed, and hence that the data sets would conform to a Poisson distribution. Prior to conducting the test, each data set was subjected to a goodness of fit test in order to establish whether this pre-condition was justified.

### A.2. Modelling the data using a Poisson distribution

Data sets from two different years were modelled to two different models: firstly (null hypothesis), that the population of the fish was unchanged in the two years, and hence that the numbers of fish observed would only differ as a consequence of random variability; secondly (alternative hypothesis), that the populations of fish did differ in magnitude between the years, and hence, on average, more fish would be observed in one year compared to the next.

The Poisson distribution describes the probability of observing a given number of fish ( $X$ ) (given that the fish

are distributed randomly), when the average number of fish observed during independent samplings is  $\mu$ . Only one parameter ( $\mu$ ) is required to define a Poisson distribution, since one of the properties of this distribution is that the mean and variance are equal to each other. In terms of the two models described above, the null hypothesis would be described by a value of  $\mu$  which would be equal for both years ( $\mu_1 = \mu_2$ ). The alternative hypothesis would be that the value of  $\mu$  would be different for the two years ( $\mu_1 \neq \mu_2$ ).

The following example shows how the maximum likelihood values for each model are calculated. Two data sets are to be compared: both have been shown to conform to a Poisson distribution. The values represent the fish counts from six independent samplings. Since  $\mu$  is the real value which describes the population, we need to estimate this value from the actual data.

Year 1 : 1, 0, 0, 1, 1, 1

Year 2 : 4, 1, 1, 2, 2, 2

For the null hypothesis (i.e., when  $\mu_1 = \mu_2$ ), the value  $\mu$  ( $\mu_0$ ) is estimated by the mean of all 12 values ( $\bar{x}_0 = 1.333$ ). For the alternative hypothesis (i.e., when  $\mu_1 \neq \mu_2$ ), these parameters are estimated by the mean values calculated for each year ( $\bar{x}_1 = 0.667$ ;  $\bar{x}_2 = 2.00$ ). It is worth noting therefore, that to describe the null hypothesis, only one parameter need be estimated ( $\mu_0$ ), whereas for the alternative hypothesis two parameters are required, one for each year ( $\mu_1$  and  $\mu_2$ ).

The likelihood of obtaining any individual value of  $X$ , for any given value of  $\mu$ , can be determined by the probability distribution function of the Poisson distribution which is as follows:

$$P(X) = \frac{e^{-\mu} \mu^X}{X!},$$

where  $P(X)$  is the probability of observing  $X$  fish on one sampling and  $\mu$  is the real mean number of fish observed per samplings. Values of  $P(X_i)$  are calculated by substituting  $\mu$  in the equation for its estimate  $\bar{x}$ , as shown in Table 3.

The maximum likelihood ( $L$ ) for each model is calculated as the product of the  $P(X_i)$  values for each model as follows:

$$\text{Model 1: } L_0 = 5.848 \times 10^{-8},$$

$$\text{Model 2: } L_1 = 4.742 \times 10^{-7}.$$

In order to compare these two models, a likelihood ratio is determined. It is a property of such a likelihood ratio that it is distributed approximately as a  $\chi^2$  distribution, and so the value of the likelihood ratio can be compared to the critical value of the  $\chi^2$  distribution at the required significance level ( $\alpha$ ) for one degree of freedom ( $v$ ) (since

Table 3

<i>i</i>	Year	$X_i$	Model 1 – null hypothesis		Model 2 – alternative hypothesis	
			$\bar{x}_0$	$P(X_i)$	$\bar{x}_1$ and $\bar{x}_2$	$P(X_i)$
1	1	1	1.333	0.3515	0.667	0.3423
2	1	0	1.333	0.2636	0.667	0.5134
3	1	0	1.333	0.2636	0.667	0.5134
4	1	1	1.333	0.3515	0.667	0.3423
5	1	1	1.333	0.3515	0.667	0.3423
6	1	1	1.333	0.3515	0.667	0.3423
7	2	4	1.333	0.0347	2.000	0.0902
8	2	1	1.333	0.3515	2.000	0.2707
9	2	1	1.333	0.3515	2.000	0.2707
10	2	2	1.333	0.2343	2.000	0.2707
11	2	2	1.333	0.2343	2.000	0.2707
12	2	2	1.333	0.2343	2.000	0.2707

one extra parameter is estimated for model 2 than model 1) and a probability determined.

The likelihood ratio (LR) (Dudewicz and Mishra, 1988) is calculated as follows:

$$LR = -2 \ln \left( \frac{L_0}{L_1} \right).$$

In this example  $LR = 4.186$ . From statistical tables, the critical value  $\chi_{\alpha, v}^2$  can be determined. In this case,  $\alpha = 0.05$  by convention.

Since  $\chi_{0.05, 1}^2 = 3.841$ , and is, as such, smaller than  $LR$ , we reject the null hypothesis, and conclude that model 2 is a more reasonable description of the data. Alternatively, where possible, an exact  $P$  value can be calculated. In this case  $P = 0.041$  which is less than  $0.05$ ; therefore, the null hypothesis is rejected. In other words,

the data supports the conclusion that the fish populations were different in the two years.

### A.3. Validation and power of the test

The power of a statistical test is the probability of rejecting the null hypothesis when the null hypothesis is not true. This power is dependent on the magnitude of the difference between the populations to be tested, the variability of those populations, and the size of samples taken from those populations. In general, in order to increase the power of any analysis, more data is required.

In order to validate the likelihood ratio test described in this paper, 1000 pairs of Poisson-distributed pseudo-datasets, with six values in each set, were randomly generated and the test applied to the pseudo-data. To determine whether the test produced the expected frequency of type I errors (the probability of incorrectly rejecting the null hypothesis), the paired pseudo-datasets were generated such that  $\mu_1 = \mu_2 = 1$ . In other words, the null hypothesis was true and any difference occurred only as a result of random variability. Under these circumstances, the proportion of type I errors ought to equal the significance level ( $\alpha$ ) chosen, regardless of that value (e.g. 5% for a significance level of 0.05). The figure shows that the frequency of occurrence of type I errors was equal to the significance level chosen at all values as expected. This indicates that the test was performing acceptably.

In order to assess the power of the test, the procedure was carried out again, except that the pseudo-data was generated such that  $\mu_1 = 0.667$  and  $\mu_2 = 2.00$ . Fig. 5 shows that the probability of obtaining a significant result for a significance level of 0.05 was 56%. It can also be seen that this figure falls dramatically as the significance level is reduced below 0.05. Further simulation showed that, as expected, the power of the test increased as the difference between that populations increased and as the number of data in each of the data sets was increased.

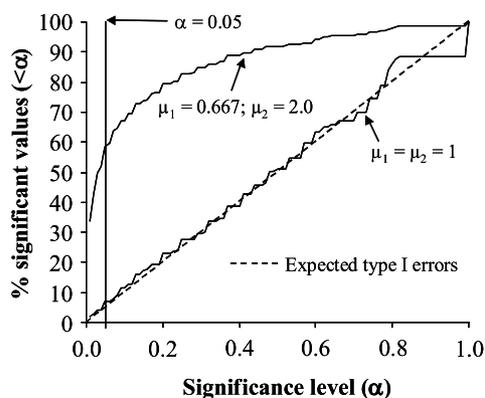


Fig. 5. Graph illustrating the probability of obtaining a statistically significant result using the likelihood ratio test when the null hypothesis is true ( $\mu_1 = \mu_2 = 1$ ) and when the null hypothesis is false ( $\mu_1 = 0.667$ ;  $\mu_2 = 2.0$ ). Data was obtained from randomly generated paired pseudo-datasets each containing six data values. For a significance level ( $\alpha$ ) of 0.05, the probability of obtaining a significant result when the null hypothesis was true was estimated to be 6.5% whereas the probability of obtaining a significant result when the null hypothesis was false (i.e., power) was 56%.

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