

CRC REEF RESEARCH TECHNICAL REPORT

DESIGN OF EXPERIMENTAL INVESTIGATIONS OF THE EFFECTS OF LINE AND SPEAR FISHING ON THE GREAT BARRIER REEF

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SUMMARY

Fishing remains the major extractive industry in the Great Barrier Reef (GBR) region. Diverse commercial and recreational fisheries are widespread, and constitute multi-million dollar industries in the region. Biological information about species targeted by fishing is necessary but not sufficient to successfully manage the fisheries and ecosystem. For justifiable, marketable, and effective management, biological information must be integrated with human demographic information, understanding of fishing practices, and estimates of the responses of fish stocks and fishing practice to changing fishing pressure. Controlled experimental manipulations of fishing pressure and management options have been recommended previously as the most effective mechanisms for assessing empirically the responses of targeted stocks, other reef organisms, and fishing practice to changes in fishing pressure. The Cooperative Research Centre for Ecologically Sustainable Development of the Great Barrier Reef (CRC Reef) provided an important institutional focus for such large scale experimental research into the effects of line fishing on the GBR, and examination of existing and future management options to maintain current fishing standards.

Computer simulations of the population dynamics of the main target species, *Plectropomus leopardus*, were used to examine the potential for large scale (whole reef) manipulations of fishing pressure. Based on recent field research, the simulations indicate that experimental manipulations can be designed such that the results will have good statistical power to detect effects of fishing and measure responses of fished stocks to protection from further fishing. Such information is not currently available for the GBR reef-line fisheries, but will be critical to future decisions about management of those recreational and commercial fisheries.

We recommend an experimental design involving 4 clusters of 6 reefs spread over 7° of latitude, between Cape Flattery in the north and the Swain Reefs in the south of the GBR. Three treatment regimes should be applied within each cluster.

- i. A *closed control* treatment represented by 2 reefs per cluster that have been closed to fishing historically and remain closed during the experiment. These reefs provide our best estimates of the behaviour of unfished, virgin stocks.
- ii. A *increased fishing* treatment, represented by two reefs per cluster that were historically open to fishing at will, and which are fished with increased intensity for one year. These reefs are then closed to fishing for 5 years. They provide our best estimates

of the capacity of already fished stocks to withstand more fishing, and the dynamics of recovery of fish stocks after protection from fishing.

- iii. A *initial fishing* treatment, in which two reefs per cluster that have been closed to fishing for 5-12 years are opened to 'at will' fishing for one year and then re-closed. This treatment will provide our best estimates of the relationship between trends in catch rate and changes in stock density, the size(s) of unfished stocks, and the responses of fish stocks and fisheries to rotational harvest strategies.

The experimental work must be complemented with sound estimates of the distribution and intensity of both recreational and commercial line fishing over the GBR region. Provision of adequate catch and effort information for the recreational fisheries is more difficult than for the commercial fleet. There have been some past attempts to estimate recreational fishing catch and effort within one year, but there are no formal longitudinal research data available. Compilation of angling club records, the recent implementation of a log book system for fishing charter boat operators, increased political focus on the recreational fisheries, and the commencement of other CRC Reef tasks to provide robust estimates of recreational reef line and spear fishing are positive steps toward the provision of essential information about recreational fishing on the GBR.

Information about the commercial line fishery will come from the QFMA compulsory log-book programme, and additional sampling of the commercial fleet as part of the experimental work and other CRC Reef Tasks. Managed carefully, such work will greatly improve collaboration between the research project and the fishing industry. This component of the work will cost little, but is essential to the sensible and acceptable transfer of results from the experiment to management of the fishery.

INTRODUCTION

Fishing remains the major extractive industry in the Great Barrier Reef (GBR) region. Diverse commercial and recreational fisheries are widespread, and constitute multi-million dollar industries in the region (Driml *et al.* 1982, Hundloe 1985, Williams & Russ 1991). Although management of fishing in Queensland and adjacent offshore waters is the responsibility of the Queensland Fisheries Management Authority (QFMA) (Offshore Constitutional Settlement 1987; Queensland Fishing Industry Organisation and Marketing Act 1982-89; QLD Fisheries Act 1989, 1993), the Great Barrier Reef Marine Park Authority (GBRMPA) effectively also manages fishing within the Great Barrier Reef Marine Park (GBRMP) by virtue of access and activity restrictions manifest in GBR zoning plans (GBR Marine Park Act 1975). Management of fishing, therefore, is shared between the QFMA and the GBRMPA.

One of the chief objectives of the Fisheries Management Authority is to conserve the targeted fish stocks at levels that provide maximum sustainable harvests. Successful management of fishing in this context will require knowledge of:

- i. the dynamics of fish stocks and their responses to fishing pressure;
- ii. the distribution and intensity of fishing effort on the GBR;
- iii. catches of targeted species; and
- iv. knowledge of the economics and dynamics of fishing behaviour.

The primary objectives of the Marine Park Authority's management are to conserve the GBR ecosystem and to facilitate sustained multiple (human) uses of the Great Barrier Reef Marine Park. Fulfilment of this broader brief will require, in addition to the above information, knowledge of:

- v. the distribution and needs of other activities that impact on or are impeded by fishing;
- vi. the secondary effects of over-fishing on other components of the ecosystem; and
- vii. ongoing assessment and revision of the management strategies implemented by the GBRMPA in the light of new or expanding activities.

In both cases, biological information about species targeted by fishing is necessary but not sufficient to successfully manage the fisheries and ecosystem. For justifiable, marketable, and effective management, biological information must be integrated with human demographic

information, understanding of fishing practices, and estimates of the responses of fish stocks and fishing practice to changing fishing pressure. Such integration has been lacking to date, and management of (particularly) the recreational fisheries in the GBR region has been relatively information-poor and theory-based rather than empirically driven. For most fisheries, empirical links between the biology of the targeted (or affected) biota and fishing practice and its management are through analyses of catch and effort data from the fisheries. In addition to the problems of being fisheries dependent, these measures provide only *post hoc* signals about the effects of fishing. Managers are playing, therefore, a constant game of catch-up involving reaction to existing problems (Hilborn & Walters 1992). Management derived from such a basis will be predisposed to failure.

In a workshop sponsored by the GBRMPA and the Advisory Committee on Research into the Effects of Fishing in the GBR region (EoFAC) (Craik *et al.* 1989), prawn trawling and line fishing were identified as the fisheries most threatening to the ecological integrity of the GBR and most in danger of economic threat through over-exploitation. Attendees concluded that controlled experimental manipulations of fishing pressure and management options were the preferred mechanisms for assessing empirically the responses of targeted stocks, other reef organisms, and fishing practice to changes in fishing pressure, effectively providing items (i), (iv), and (vi) above. This approach would provide insights to the effects of increasing fishing pressure before such increases occurred widely. Hence, experimental manipulation of fishing activities provide the potential to develop management strategies pro-actively rather than re-actively.

In 1990, Prof. Carl Walters and Dr. Keith Sainsbury were commissioned by the Great Barrier Reef Marine Park Authority to examine design options and logistic considerations for such experiments in the GBR region. They discussed the potential fishery and ecological consequences of fishing that should be considered in the region, and recommended the development of a multi-institutional research programme to examine the effects of trawl fishing and line fishing and their interactions on the GBR (Walters & Sainsbury 1990). Despite the benefits of and interest in the proposal, however, such a programme was not begun, mostly because of restricted funding and the lack of a clear institutional focus for the work.

In 1992 the Federal Government approved the establishment of a Cooperative Research Centre for Ecologically Sustainable Development of the Great Barrier Reef (hereafter 'the CRC'), which began operations in July 1993. Research into the effects of line and spear fishing was one of the projects (hereafter ELF project) included in the CRC proposal and attracted considerable

dedicated institutional support in cash (GBRMPA, QFMA) and in kind (Australian Institute of Marine Science (AIMS), GBRMPA, James Cook University (JCU), Queensland Department of Primary Industries (QDPI)) (Anon 1992, Anon 1993). The principal of large (reef) scale experimental manipulations of fishing pressure to examine the effects of fishing remained one of the methodological cornerstones of proposed research into the effects of line and spear fishing (now the CRC ELF project).

Consistent with the scope of the CRC, the initial concept was explicitly focused on recreational reef fisheries. Since the recreational and commercial line fisheries generally target the same species, have access to the same resource spatially and temporally, use similar fishing gear, and have been estimated to harvest about the same annual catch, (Craik 1989, Gwynne 1990, Blamey & Hundloe 1992, Higgs 1993, Davies 1993, 1994), however, it is essential that management research explicitly consider both groups. In practice, it will be difficult or impossible to demarcate between the recreational and commercial line fisheries. The CRC ELF project, therefore, inevitably will (and should) address issues salient to both fisheries, but it was not intended to cover research into the trawl or other commercial reef fisheries. Thus, the brief of the CRC project differed from that considered by Walters & Sainsbury. Further, the budget for the CRC project was substantially less than that anticipated by Walters & Sainsbury, and considerable work relevant to potential experiments had been done since 1990. This project arose, therefore, out of the need to review Walters' & Sainsbury's (1990) recommendations in the context of the clear brief of the CRC, the available funding and expertise, and the results of recent research on species targeted by reef line fisheries, especially coral trout (*Plectropomus* spp.). At the request of CSIRO (Cleveland Marine Laboratories) and QDPI, we considered also experimental design options that would facilitate the development of a large scale experiment to examine the effects of trawling on reef and inter-reef fisheries, without compromising the objectives of the ELF project.

Thus the objectives of the project were:

- ?? To review previous experimental designs for research into the effects of fishing on the GBR;
- ?? To develop experimental designs for research into the effects of line and spear fishing given:
 - i. available data on fishing in the GBR region and demographics of targeted species;
 - ii. the brief of the CRC, with a focus on line and spear fishing;

- iii. the logistic and financial resources available to the CRC;
 - iv. management and surveillance strategies likely to be available to establish and monitor reef-scale manipulations over the next 5-7 years.
- ?? To recommend objectives, strategies, and budgets for experimental manipulations of line and spear fishing on the GBR at scales appropriate to potential management strategies, features of the reef-line/spear fishery, and the population dynamics of exploited species.
- ?? To consider options for integrating experimental designs for research into the effects of line and spear fishing with potential research into the effects of demersal trawling on the GBR.[?]

[?] The specific objectives, geographic and temporal scope, logistic and funding of such trawl research will not be considered in detail here.

PREVIOUS PROPOSALS FOR EXPERIMENTAL FISHING ON THE GBR

Three previous proposals for experimental manipulations of fishing pressure in the GBR region have been submitted or attempted in the GBR region. Beinssen (1988, 1989a,b, 1990) undertook two field programmes to estimate fishery statistics for, mainly, coral trout and to assess the likely utility of the current zoning strategies on the GBR. In the first, he took advantage of the opening of Boulton Reef (in the Capricorn-Bunker Group, southern GBR) to fishing following a 3.5 year closure. He estimated changes in catchability during initial fishing of a 'virgin' stock, and assessed the potential for substantial depletion of reef-associated populations as a result of line fishing on the GBR. He involved commercial, recreational, and charter-boat fishers in closely monitored fishing over the fourteen days following opening of the reef, having previously released about 1700 tagged fish on the reef. His results (Beinssen 1988, 1989a) indicated that:

- i. Stock size was reduced by about 25% during the 14 days of intensive fishing;
- ii. Catchability declined far more rapidly than stock size after the first few days of fishing;
- iii. Coral trout were relatively sedentary on the reef over (at least) short periods.

Conclusions ii. & iii. were supported subsequently by tag-release-recapture work combined with sustained fishing (for tag and release) and underwater visual surveys by Beinssen at Heron Island (Beinssen 1989b, 1990).

Despite the restriction of Beinssen's work to only single reefs in the far-southern section of the GBR, his work provided valuable background information for future research involving experimental line fishing. His results clearly suggested that substantial stock reductions are feasible with manageable amounts of fishing, that fishing should probably be pulsed rather than continuous, and that individual reefs may be satisfactory experimental units. He also notes that commercial line fishers generally fish reefs for only 1-2 days at a time, consistent with what would be expected given rapid declines in catchability as the 'feeding phase' fish on a reef are taken off (see also Gwynne 1990). Beinssen's data also indicated that dedicated work is required to document clearly the relationships between abundance, fishing, and catchability, since it cannot be assumed that catchability remains constant with changes in abundance. Understanding the relationship(s) between catchability, fishing practice, and stock

abundance is critical to the interpretation of user-supplied fishery dependent records, such as log book data, and their use in stock assessment procedures (Hilborn & Walters 1992).

Mapstone *et al.* (1989) proposed the manipulation of fishing pressure and zoning status at eight mid-shelf reefs off Innisfail. The experiment was proposed to take advantage of the forthcoming review of the zoning plan for the Cairns Section of the GBRMP. All reefs had been open to fishing historically, and Mapstone *et al.* proposed an orthogonal experimental design involving deliberately fishing four of the reefs over a 3-6 month period and then closing (during revision of the zoning plan) 2 of the heavily fished and 2 of the control reefs to all further fishing. Visual survey data on abundances of targeted and non-targeted species were to be collected before, during, and for several years after the manipulation of fishing pressure. Catch-effort data and age and size structure data for targeted species were to be collected only during the (controlled) fishing manipulations. The design was predicated on the assumptions that i) zoning half of the reefs as non-fishing areas would effectively reduce or eliminate subsequent fishing pressure; and ii) fishing would continue on those reefs that were left open to fishing, even where it was public knowledge that heavy fishing had previously occurred. The authors proposed to deliberately sponsor fishing, if necessary, to ensure the second assumption was met, but made no comment about the likelihood of the first assumption being satisfied.

The proposal by Mapstone *et al.* (1989) did not consider in detail the logistics of manipulating fishing pressure. The budget allowed little money for direct support of fishing, and it probably would have proved difficult to achieve the desired level of fishing on all four reefs. A second weakness of the proposal was its local geographic focus. Although slated as ‘a simple preliminary experimental study’ (Mapstone *et al.* 1989, p2), there was no basis from which to infer the relevance of the work to areas other than the Cairns-Townsville region. The proposed work was weak also in that no comparison of age and size structures or recruitment of targeted species between control and experimental reefs was included, and so the effects of fishing and closure were to be assessed only by changes in population density.

A more ambitious experimental programme incorporating manipulations of reef-line fishing and inter-reef trawling in a split-plot design spread over three sections of the GBRMP was proposed during the above mentioned workshop (Craik *et al.* 1989). The proposal involved two ‘clusters’ of five reefs in each of the Cairns, Townsville, and Mackay-Capricorn sections

of the Marine Park. Each cluster was comprised of five adjacent reefs. Two reefs in each cluster were to be closed to fishing, two were to be open to fishing, and the fifth was to be 'split-zoned', half being open and half being closed. One of each pair of clusters in each section was to be open to inter-reef trawling, and the other cluster in each pair was to be protected from trawling. All treatments were to be imposed by zoning regulations during reviews of the relevant zoning plans, with the result that the treatments would be imposed sequentially as each section of the GBRMP was rezoned. This would have meant that regional (section) effects in the work were inherently confounded with starting time and rezoning of the sections. There is currently a 2-5 year lag between successive rezoning of the sections of the GBRMP. The treatment regimes on all reefs and clusters were to be reversed after five years, resulting in a 'cross-over' design. The proposal did not involve deliberate enhancement of fishing pressure. Although flagged as a 'multi-institutional' project, none of the locations, budgeting, logistic, or institutional arrangements for the work were discussed in detail. Queensland Department of Primary Industries submitted a detailed expression of interest in some of the work later in 1989 (Anon., 1989).

The above design was revised by Walters and Sainsbury (1990), who presented considerably more detail about the logistics, locations, institutional contributions, and costing for the work. They also considered the feasibility of a range of experimental designs involving different numbers of clusters (4, 6, 8, 10, and 16) of different numbers of reefs per cluster (8, 5, 4, 3, and 2 respectively). The basic design framework was that which was derived at the 1989 workshop, except that no 'split-zoned' reefs were involved. Three line fishing treatments were considered desirable: i) reefs historically closed to fishing, which would remain closed; ii) reefs historically open to fishing which would be closed at the commencement of the experiment; and iii) reefs historically open to fishing which continued to be exposed to fishing (where there were sufficient reefs within each cluster). The principles of 'staggered starts' to the work, and treatment cross-overs after 5 years, were maintained throughout Walters' and Sainsbury's work. They assessed the merits of various design options by modelling the behaviour of targeted fish populations and their recruitment dynamics, fishing on the GBR, and the effects of experimental regimes on survival, and inter-reef migration of adult fish. Walters and Sainsbury recommended that such an experiment should proceed as a multi-institutional project, with work being done on at least 8 clusters of 45 reefs over at least 10 years (Walters & Sainsbury 1990).

Whilst Walters' and Sainsbury's review was thorough and involved considerable consultation with researchers, management agencies, and fishing industries, the work they proposed was logistically very difficult and extremely expensive (~\$2.1M pa). As the authors emphasised, their recommendations also were pinned on a number of assumptions which at that time were untested. In particular, the reef-scale line fishing treatments rested on the assumption that migration of adult target species among reefs was less than 25% per annum, and the cluster scale trawl treatments assumed roughly similar inter-reef habitat characteristics and trawling history over all clusters. They flagged several other potential problems that could undermine their proposed experiment, but stated that 'the basic scientific answer [to those problems] is to provide adequate replication at the various spatial scales of measurement and treatment' (Walters & Sainsbury 1990, p10).

EVALUATION OF POTENTIAL EXPERIMENTAL DESIGNS

The remainder of this report is devoted to our evaluation of options for experimental designs for the CRC ELF project. Our main focus is on the statistical properties of different design options, as estimated from dynamic population models. The models were tuned by reference to real data for the main species targeted by GBR fisheries, the common coral trout (*Plectropomus leopardus*). We also consider non-statistical considerations that ultimately would be expected to guide the choice of design and its implementation. We do not include detailed discussion of the implementation, however.

OBJECTIVES OF FUTURE REEF-SCALE EXPERIMENTS

The overall objectives of the CRC Effects of Fishing project are:

- i. To document the distribution and intensity of reef-based fishing catch and effort and patterns in relative abundance of fish stocks.
- ii. To understand the distribution and intensity of fishing that existing fish stocks and reef communities can sustain *via*:
 - ?? Investigations of demographic characteristics of targeted species; and
 - ?? Experimental manipulations of fishing effort and management strategies.
- iii. To evaluate the efficacy of current management practices, specifically zoning strategies, with respect to the sustainable management of reef fishing at levels consistent with conservation of stocks and the wider reef ecosystem.
- iv. To document the limits of fishing induced changes in fish catch and other aspects of reef use that would be acceptable to reef users.
- v. To recommend management strategies for the future regulation of fishing such that fish stocks, ecosystem function, and yields to fisheries will be conserved.

'Experimental manipulations of fishing effort and management strategies' have the potential to provide information relevant to objectives ii-v. Accordingly, we recommend seven specific objectives for large-scale experiments on the effects of line fishing on the GBR[?].

1. To estimate the effect of line fishing on the abundance and demography of index species (such as coral trout) that are directly impacted by fishing.
2. To describe the effect of line fishing on the abundances of index species that are not directly impacted by fishing but may be affected indirectly, through ecological processes such as predation and competition.
3. To determine the dynamics of recovery of index reef populations when reefs are closed to fishing and the responses of catch rates to recovery of populations protected from fishing.
4. To document the responses of catch rates for the reef line fisheries to changes in abundances of index target species under increasing fishing pressure.

[?] The first three objectives paraphrase those stated by Walters & Sainsbury (1990).

5. To test the utility of CPUE (Catch Per Unit of Effort) and visual survey as methods of use for stock assessments for the GBR, specifically assessing their sensitivity to changes in stock density.
6. To estimate regional patterns in the effects of reef-scale closures to fishing on abundance and catchability of index target species.
7. To provide an empirical basis for modelling the dynamics of fishing and fish stocks on the GBR in response to changing fishing pressure and alternative management strategies.

Selection of Design Alternatives

Potential Treatments

The spatially patchy character of the GBR and the large number of discrete patches of reef habitat available (~2,500 reefs) provide considerable scope for large-scale experimental manipulations. Numerous experimental treatments could be considered to examine the effects of fishing and the recovery dynamics of exploited stocks. Options we considered were:

1. Reefs that had been closed to fishing historically, and would remain closed throughout the experiment. These reefs would represent our best estimate of the dynamics of virgin stocks on 'pristine' reefs - effectively the control situation;
2. Reefs that had been open to ambient fishing historically, and would remain open throughout the experiment. These reefs would measure the effects of ambient fishing pressure during the experiment;
3. Reefs that were open to fishing historically and were closed to fishing near the start of the experiment;
4. Reefs that were open to fishing historically, were then fished intensively for some period, and then closed to fishing;
5. Reefs that were closed to fishing historically and were opened to fishing near the start of the experiment for some period (and then re-closed).

Clearly, the greatest amount of information for anticipating the capacity of the reefs to sustain increasing fishing pressure would arise from the contrast of treatments 1, 4, and 5. We included options 1 and 4 in all designs. We also included either treatment 2 or 3 in some cases, although including both treatments 3 and 4 in designs involving local replication of treatments was considered unlikely to be feasible in reality because the large number of reef closures involved (? 4 in each region) would precipitate untenable public opposition to the work.

Treatment 5 is problematic also because of the potential for public opposition to work involving the deliberate fishing of (previously) protected reefs. Walters & Sainsbury (1990) discussed two arguments against including treatment 5: '(1) few such reefs [historically closed to fishing] are available in the GBR, and these reefs are most valuable as places to measure the long term effect[s] of closure to fishing; and (2) the initial transient responses to opening a reef to fishing (high fishing pressure, rapid depletion of larger fishes) are obvious and are already fairly well understood.' Their first point is one of degree: out of 2716 reefs in the GBR Marine Park, there are 447 Marine National Park 'B' reefs, 30 preservation zones, and 3 zones for scientific research only. These reefs represent 17.67% of reefs in the Marine Park, and all normally are closed to fishing. In most cases, their original selection for protection was not based on any special features, and often resulted from the exclusion of other options. Provided that the numbers of reefs to be opened for fishing is kept small, we consider that the value of information to be gained from fishing them will outweigh the 'costs' of reducing (slightly and temporarily) the number of 'closed' reefs on the GBR. Given that currently open reefs would likely be closed to fishing in treatment 3 or 4, there might in fact be no reduction (and possibly an increase) in the number of closed reefs provided the 'opening' and 'closing' of reefs was managed carefully. Finally, if treatments 3 or 4 alone are considered the result is likely to involve economic and social impacts on existing fishers of the GBR. Opening some reefs to fishing concurrently with closing others would minimise such impacts.

Walters' & Sainsbury's second argument (above) is more speculation in relation to the GBR line fisheries than substantiated argument. It is to be expected that opening closed areas to fishing will result in an initial 'burst' of fishing pressure, possibly with substantial reductions in stock density. Beinssen's work (1989a,b, 1990) indicates, however, that in such events catch rates are likely to decline to unacceptable levels far more rapidly than stock density, with the result that fishers rapidly lose interest in fishing in the 'new' area. Despite incentives to keep fishing, fishers harvested only 25% of the (theoretically) available stock on Boulton Reef. This phenomenon is consistent with anecdotal evidence from the commercial line fishery in the GBR, which indicates that most commercial fishers fish an area for only 1-2 days before moving to another area. The reasons for moving are cited as: i) drop in catch rate; and ii) crew dissatisfaction with fishing over ground that has been covered already. More work is needed to satisfactorily describe what does (or does not) happen when new territory is made available to the reef-line fisheries, especially if any rotational or periodic harvest regimes are to

be considered for management of the fisheries. Further, the heightened interest in fishing new areas is likely to provide the best environment in which to describe empirically the relationship between changes in catch rate and changes in stock density.

Constraints on Design Options

Unlike Walters and Sainsbury (1990) we were working within known boundaries, and our choice of experimental design options was constrained accordingly. Several factors were considered at the outset when defining the scope of our evaluations.

Duration

The CRC has guaranteed funding until June 30, 2000. Funding for CRC work beyond that date will depend mainly on continued industry support, and the results of work to that date. We considered experimental design options, therefore, only within the realm of secure funding - *i.e.* the experiments were expected to run for 6 years, and all manipulative treatments had to be established within that period. Whilst all the designs we considered could be extended beyond that period given sufficient funding, and most would benefit considerably from continued monitoring, we did not consider the form(s) of such extension(s) in detail. Further, it was clear that the lead-time involved in any experimental manipulations and /or reef closures would mean that (at least) the first year of the project would provide only baseline data.

Logistics

Logistic considerations were important mainly from the perspective of i) the expected normal dynamics of the fishing fleet(s); ii) measuring inter-reef movement of fishes; iii) facilitating future trawl research; and iv) cost-efficiency. Logistic considerations mainly influenced the gross experimental structure, particularly with respect to the arrangement of treatment reefs in the experimental layout. The statistically desirable strategy was to choose (randomly) experimental reefs from large areas (*e.g.*, within regions, or over several regions), without regard to their proximity to each other. An alternative approach was to select 'clusters' of neighbouring reefs in each region, with each line-fishing treatment applied to at least one reef within each cluster. We considered only the latter option, for three reasons.

Firstly, a random distribution of reefs would increase considerably the logistic difficulty and cost of imposing trawl fishing treatments over an alternative design framework in which experimental reefs were grouped into 'clusters' of neighbouring reefs. In the latter case,

trawling between reefs within a cluster would effectively result in a trawled treatment applied to several line-fishing treatment reefs, with trawling around the perimeter of the cluster being the only effort that applied directly to only one reef at a time (Walters & Sainsbury 1990). Such a treatment structure seems appropriate because it is unlikely that commercial trawling would occur around isolated reefs, but would be a larger-scale, regional operation affecting whole groups of reefs at once. Further, to assess line fishing - trawling interactions when line fishing treatments were allocated strictly at random, far greater trawling would be required because trawling around any one reef would have no influence on the other line fishing treatment reefs. Thus, the clustered approach seemed more relevant to the expected real effects of trawling, and the split-plot design a more economic structure within which to examine line-trawl interactions in the future.

Secondly, the logistics of assessing inter-reef migration of fish to/from experimental reefs would be much simpler (and less expensive) if reefs with different treatments were arranged in 'clusters'. With all experimental reefs in a region being neighbours, the need to sample both several source and destination reefs for migration would be fulfilled by simply sampling all experimental reefs in a group. To estimate inter-reef migration of fish to/from experimental reefs in a fully randomised design would mean sampling several (non-experimental) reefs surrounding each reef on which experiments were to be done. The total number of reefs at which at least some sampling would be required would be unfeasible under these circumstances.

Thirdly, randomising reefs over larger areas would almost certainly increase steaming time among reefs, and, therefore, reduce the time available for research within the constrained budget. Similarly, orchestrating the cooperative participation of the fishing fleets in research and monitoring of their activities on experimental reefs would be far more difficult and less cost-effective under a strictly randomised design.

Generality of Results

In workshops held in 1990, 1992, 1993, and 1994 divergent opinions arose over the spatial emphasis of fishing experiments. At one extreme, management agencies and some researchers favoured having the experiment spread over as wide an area as possible so that the results could be seen as relevant to much of the GBR. At the other extreme, some researchers favoured concentrating effort locally and deriving more detailed results for those

places than the lower resolution data that would arise from spreading limited effort over larger areas. We considered designs encompassing the range of opinions in order to assess whether there were specific analytical consequences of either detailed localised experiments or less detailed widespread experiments.

Availability of suitable reefs

The scope of the design was also likely to be limited by the availability of reefs that:

- i. would satisfy the conditions for some of the above experimental treatments, especially those involving a history of closure to fishing;
- ii. were large enough to be relevant to most of the reefs on the GBR;
- iii. were small enough to allow the imposition of increased fishing effort over their entirety;
- iv. were relatively isolated by at least 500-1000m of non-reef, deep water habitat; and
- v. were within areas where we might expect to be able to encourage increased fishing pressure from recreational fishers as well as commercial fishers, and which were within 1 day steaming of convenient port and cold-storage facilities. Proximity to ports and refrigeration facilities was important to ensure access to recreational and charter vessel fishers and facilitate savings in the imposition of increased fishing pressure through the sale of commercial catch from experimental reefs.

Impacts of Experiments

The experiments we considered would involve the closure of reefs to fishing for up to five years, following localised intensive fishing, and possibly the opening of currently protected reefs for limited periods. Both the intensive fishing and the closures would have impacts on the recreational and commercial fishers who previously utilised those 'fished and closed' reefs. It was important, then that we minimised as far as possible the concentration of experimental treatments in one area and considered options for compensating for lost access to resources through the opening of nearby reefs.

Cost

It was clear that cost would be a conspicuous constraint on design options, given the offshore locations for all fieldwork, the high costs of charter vessels to support sampling experimental reefs, and the likely costs of imposing exaggerated fishing pressure and monitoring fishing effort and catch. The intensity of sampling per experimental reef per year clearly would be

constrained by cost as the number of experimental reefs increased. We considered as a minimum sampling requirement the need to obtain: i) basic abundance and recruitment data from all experimental reefs in each year; ii) estimates of age and size structures of the principal target species in at least some years; and iii) estimates of catch rates (CPUE) and responses of fishers to fishing success on experimental reefs in all years and repeatedly during stock reductions.

Designs Examined

We assessed a number of alternative experimental designs considered feasible within the above set of constraints. We estimated that it would be feasible to collect abundance and age-structure data from all reefs in each year on, at most, 12 reefs, assuming also that exaggerated fishing was imposed over one year on no more than six reefs. The maximum number of reefs that could be sampled annually for abundance data whilst still providing sufficient data to address the objectives of the work was 24. In this case, age-structure information would be obtained from all reefs only in the first and last years and controlled fishing would apply to at most 12 reefs. Thus, we considered experimental designs involving 12-24 reefs. Given that we considered only designs with reefs grouped into clusters (above), we considered the design configurations shown in Table 1.

Table 1: Experimental designs assessed for the CRC Effects of Line Fishing Project. The numbers in ‘TREATMENT’ columns are the numbers of reefs in each treatment in each cluster.

Abbreviations: **C-C**=reefs closed historically and during experiment; **O-Cl_{ij}** =reefs historically open to fishing but closed after year *i* or *j* of the project; **O-P_{ij}-C**=reefs historically open to fishing, ‘pulsed’ with intensive fishing in years *i* & *j* of the project, and closed to fishing thereafter; **C-P_{ij}-C**=reefs historically closed to fishing, ‘pulsed’ with intensive fishing in years *i* & *j* of the project, and closed again to fishing thereafter; **? Reefs**=total number of reefs in the experiment; **n/reef**=number of sampling units (data) per reef.

Cluster s	Reef s	TREATMENT			? Reefs	n/reef
		C-C	O-P _{2,3} -C	-		
2	6	2	2,2	-	12	24-60
3	4	2	1,1	-	12	24-60
4	3	1	1,1	-	12	24-60
6	2	1	1,-	-	12	24-60
4	4	2	1,1	-	16	24-60
5	4	2	1,1	-	20	24-60
4	6	2	2,2	-	24	24-60
6	4	2	1,1	-	24	24-60
		C-C	O-P _{2,3} -C	O-Cl _{2,3}		
2	6	2	2,-	2,-	12	24-60
2	6	2	1,1	1,1	12	24-60
		C-C	O-P _{3,5} -C	C-P _{2,4} -C		
4	6	2	1,1	1,1	24	24-60

Computer Simulations

Like Walters & Sainsbury (1990), we used computer models of the population dynamics of target species, ambient fishing pressure, and experimental treatment regimes to evaluate potential experimental designs. The models allowed us to examine the expected sensitivity of proposed analyses of basic field data to detect and measure the (known) effects of various fishing regimes applied through different experimental designs. The criteria by which experimental designs were compared were i) their statistical power to detect the presence of treatment effects of known magnitude; and ii) their robustness to ‘nuisance’ sources of variation before and/or during the experiments. Nuisance variation here means any source of variation that is beyond our control and which might obscure the effects of fishing treatments in the field data.

The utility of this approach rests on the assumptions that: i) the models generate a reasonable representation of the population dynamics of the species to be studied; ii) the range of experimental treatments simulated reflect those that can be applied in the field; and iii) the

nuisance variations introduced to the population dynamics are realistic in both spatial and temporal character, and magnitude, and represent the main perversities that might occur in the field. In order to meet these assumptions, we set the parameters of the models (see below and Appendix 1) such that model output reflected the characteristics observed in real data-sets from the GBR region. The chief advantage of such an approach was that it allowed us to examine the robustness of various designs to an array of alternative hypotheses about the population dynamics of the target species (or systems), fisheries behaviour, and management strategies.[?] The objective of our simulations, therefore, was to identify which, if any, sets of nuisance variations would be likely to jeopardise the capacity of the experiment to produce unequivocal results. Decisions about whether and/or how to proceed with the work could then be based on judgements about the likelihood that such adverse scenarios would arise.

We based our simulations on the 'REEF' programme authored in Quick BASIC(?) by Walters and Sainsbury (Walters & Sainsbury, 1990). The REEF programme comprises procedures for simulating hydrodynamic dispersal (of passive particles) and fishing pressure over the GBR Region, population dynamics of selected reef organisms, outbreaks of *Acanthaster planci* (Crown-of-Thorns starfish), and various experimental and/or management regimes applied at a grid scale of 10km x 10km. Some statistical analyses can be done, and simulation data can be output for use by other software. We modified the REEF programme to allow greater control over variation in recruitment and mortality regimes applied to simulated populations and to cater for our own approach to design evaluations (see below). We were not interested in COTS outbreaks or in simulating fishing pressure over the entire region, and did not use those aspects of the software. Further, although the hydrodynamic dispersal elements of the original model were left intact, they were effectively inconsequential in our implementation. We preferred to control directly the nature of variation in recruitment at each reef rather than generate that variation from what was a simplified dispersal model encompassing many untested assumptions. In essence, therefore, we built on the population dynamics, localised fishing, and experimental treatment aspects of the REEF model, but disabled those more tenuous components that dealt with interactions between line fishing and trawling, line fishing and *A. planci* outbreaks, line fishing and community-wide effects, and the dispersal characteristics of reef fish larvae. A corollary of these exclusions was that the [notional] 10km x 10km grid scale of the REEF model was not critical to our results, because

[?] We were not interested, at this stage, in modelling management strategy or fishing behaviour except as tools for imposing experimental treatments. Modelling these dynamics (& others) will be central to

the size of reefs or their distances apart did not affect their similarity or differences in response(s) to fishing or treatment regimes, or in the population dynamics of target species. We specified all such relationships explicitly, rather than generate them by simulation (as Walters & Sainsbury had done).

Experimental treatment effects and the effects of background fishing on populations of coral trout were imposed by varying the mortality regimes applied at particular reefs. Estimates of existing fishing mortality were derived from existing data, whilst estimates of fishing mortality to be imposed during experiments were at our discretion. We believe they represent a reasonable approximation of what can be achieved in practice, given prior experience and some knowledge of current fishing practices (Beinssen, 1989, 1990, Davies 1994, Gwynne 1990, Higgs 1993, pers. obs.). The nuisance variation we considered included stochastic and systematic variations in recruitment, stochastic variations in natural mortality and fishing mortality, and sampling error. The main features of the parameters varied in our simulations are discussed below, and the details of how they were applied in the computer models are given in Appendix 1[?].

Population Dynamics

The population dynamics models comprised three main components:

- ?? modelling recruitment to reefs;
- ?? modelling post-recruitment mortality;
- ?? modelling migration.

The population of fish on each reef at each iteration of the model (= 1 year) was generated by:

- i. Generating a value for larval supply to the reef;
- ii. Applying a reef and time dependent variation to that base number;
- iii. Multiplying the resultant number (of larvae available for settlement) by a survivorship representing transition to abundance of juveniles at the end of the first year on the reef;

the extension of experimental results to recommendations for management.

[?] In the following discussion, directions to Appendix 1 are given for those readers interested in model details. The references are given as (A1:i), where *i* is the page number at the *base* of each page in Appendix 1.

- iv. Applying mortality to the 1yo, 2yo, and adult (?3yo) 'cohorts' extant on that reef from previous iterations;
- v. Adjusting the numbers of adults for immigration and emigration; and
- vi. Incrementing the ages of all sub-adult cohorts.

Recruitment and mortality (both natural and fishing mortality) were the main sources of inter-reef and inter-annual variation in population dynamics, whilst migration was treated as a spatially and temporally constant rate. Each iteration of the models produced outputs of the numbers of 1yo, 2yo, and adult (?3yo) fish on each hypothetical reef. These numbers represented the populations available for sampling, and included only variation arising from presumed biological and stochastic natural processes. These numbers were then multiplied by a randomly generated number to mimic the effects of sampling variation on field estimates of abundances. Whenever stochastic variation was added in the model, limits were applied to the result based on available empirical evidence, though we often increased the upper limit on variation so that results of the simulations were conservative (*i.e.*, lead to cautious rather than liberal interpretations of the likelihood of success of the experiment).

Initialisation

'Populations' of fish on reefs were initialised by seeding each population with an arbitrary number of (adult) individuals, and then running the population dynamics simulations for 30 iterations (=years). This was the minimum time taken for populations to stabilise when driven only by the deterministic components of the model, without stochastic variation. During the initialisation period, the (future) experimental reefs were subject to whatever systematic and stochastic sources of variation in population process, including existing closure status and fishing pressure, that were to be present during the experimental trials, except the experimental treatments planned for years 31-36.

Larval Supply

The major sources of input for the modelled population on each reef was a value for larval supply to that reef. Larval supply to each experimental reef was generated from three sources: i) 'self-seeding' from spawning on that reef; ii) supply from spawning on adjacent experimental reefs; and iii) supply from the background pool of larvae spawned on all reefs in the GBR. Walters and Sainsbury (1990) generated these values from simplified dispersal models encompassing the entire GBR, and then (optionally) imposed 'waves' of additional

recruitment stochastically at each iteration (A1:ii). We took a slightly different approach. Although we modelled larval supply as the same three sources, we did not utilise any deterministic patterns in larval supply predicted by Walters' and Sainsbury's dispersal model. Instead, we chose to impose specific patterns among reefs, clusters, and years explicitly. Thus, we were not examining the experimental design options for particular reefs in particular locations, but treating our experimental reefs as strictly hypothetical sets where we could examine the implications for experiments of different scenarios that might arise on the GBR, but are at present unknown. This approach seemed justified given that we have little knowledge of the real dispersal-links between reefs on the GBR.

Each component of larval supply was calculated by a Beverton-Holt relationship relating the abundance of settlement-competent larvae to (simulation) abundances of adults on each reef (for components i. & ii.) or the average per-reef abundance of adults on all reefs (for component iii.) (A1:iii). In our implementation of Walters' & Sainsbury's model, however, planktonic life was expected to be about 30 days, and the probability of larvae being retained in the vicinity of the natal reef was set at 0.05. Hence, the potential for local stock-recruitment relationships was low and the contributions of larvae from self-seeding and from neighbouring reefs were negligible (A1:iii). Two parameters were important in the Beverton-Holt relationship: the product of fecundity and survival through planktonic dispersal, and the 'carrying capacity' of reef waters for settlement competent larvae. We set the fecundity*survival parameter to 1 in all our work, effectively indicating that adult populations, on average, had the potential to reproduce themselves each year. The larval carrying capacity was set at one of two values which mimicked either 'high' carrying capacity of larvae and a strong link between adult abundance and larval supply, or 'low' carrying capacity and little deterministic effects of (global) adult abundances on larval supply, except when adult abundance was very low.

We also controlled the consistency in background larval loading among reef clusters, whether the larval carrying capacity was set low or high. This was done by setting a 'cluster scaling' parameter (A1:v). When set to 1, this parameter dictated that all clusters had the same larval loading from background sources, and, therefore, effectively had the same seed value for larval supply in a given year (since local supply was negligible). Setting the cluster scaling to n meant that background larval supply varied n -fold among clusters, in a north-south low-high gradient. This might be expected over much of the GBR because the influence of the East

Australian Current on the hydrodynamics of the GBR increases south from about Cairns, and so more southerly reefs might be expected to experience increased exposure to larvae competent to settle as a result of accumulated supply from an increasing number reefs to their north (see also *AI:iii*).

The above processes were deterministic. To model stochastic variations in larval supply, we multiplied the (deterministic) larval supply at each reef by a log-normally distributed value, generated for each reef in each year (*AI:vi*). We used a log-normal variation because for most reef fish species recruitment is characterised by moderate variation around relatively low values and occasional very large pulses. The multiplier comprised three sources of variation: i) an overall average inter-annual variation; ii) variation among clusters in that mean inter-annual variation; and iii) variation among reefs within clusters in that mean inter-annual variation. Each of these components could be user-controlled, and we also allowed selection of whether clusters and/or reefs behaved independently or coherently through time. Thus, we could specify a value for inter-reef variation in the (inter-annual) recruitment variation, but specify that the inter-reef component was similar for all reefs within a cluster. That is, if reefs were to be considered coherent, then a given year would be ‘good’, ‘bad’, or ‘mediocre’ for all reefs in that cluster, even though they would not all have the same value for larval supply. Hence, we were able to simulate situations ranging from no variation in larval supply to situations in which larval supply varied among years independently or coherently at both cluster and reef scales.

Recruitment

Translation of the larval supply value for each reef to a recruitment value was also via a Beverton-Holt relationship (*AI:vii*). Again, two parameters were critical: the rate of survival from the larval supply stage to the end of the first year on the reef (which here defined the point of recruitment[?]), and the recruitment carrying capacity of the reef. We set the average rate of survival from larval stage to age 1 arbitrarily at 0.4. The recruitment carrying capacity was varied between a ‘high’ value, which would result in a strong relationship between larval supply and recruitment, and a ‘low’ value which would result in a strong influence of reef-resident juveniles and adults on recruitment. The recruitment capacity was scaled by two-fold over the length of the GBR, mainly as a reflection of the cline in estimated abundances of

coral trout and the expected influence of the southerly flowing hydrodynamics of much of the GBR. In addition, however, we allowed the recruitment capacity to be homogeneous among reefs within clusters or to be scaled over an m -fold range, such that certain reefs consistently had greater capacities for recruitment than others (*A1:viii*). Because of the non-linear way in which the recruitment capacity affected the translation of larval supply into recruitment, this meant that i) those reefs with a higher recruitment capacity would have a tighter relationship between larval supply and recruitment; and ii) the m -fold scaling of recruitment would result in a slightly less than m -fold scaling in realised recruitment. Because we would not know about any scaling effects within clusters at the time of starting the experiment, we allocated treatments to reefs within clusters at random for each run of the model. Thus, the effects of reef-scaling would be expressed as an effect on the uncertainty of detecting effects (because of random correspondence of reef-level scaling with experimental treatments), rather than as the effects of having systematically confounded scaling with treatments within clusters.

Mortality

Average annual mortality from larval supply to recruitment was 0.6, whilst average mortality for the next two years were 0.4 and 0.3 respectively. Thereafter, average natural mortality was set at 0.17. The latter value was estimated from field data (below), the first value was arbitrary, and the middle two were set such that the relative strengths of cohorts at age 9 (for fished reefs) and 12-14 (for unfished reefs) matched those observed in the available field data. In setting these values we assumed that rates of mortality decreased with age in the juvenile population. Actual mortality applied to each age group at each iteration was derived from applying reef and time dependent stochastic variation to the above mean rates, which were common to all reefs and times (*A1:viii*). On reefs subject to fishing, an additional mortality of 0.17 (average) was applied to the adult population, and this value was also subject to a stochastic variation among reefs and years. The magnitude of variation in natural and fishing mortality was user defined. We considered only two values for those variations. Variations (=sd of estimators) in natural mortality were set at either 0.05 or 0.03 times the average rates of mortality, whilst variations in fishing pressure was set at 0.25 or 0.19 times the average rate. Note that fishing mortality was only applied to that proportion of the adult population considered vulnerable to fishing (*A1:ix*).

[?] Recruitment in this context meant entry to the reef-associated (demersal) population, rather than entry to the legally fishable population (= recruitment to the fishery). Recruitment to the fishery occurred at

Migration

Migration was represented by a user defined proportion of reef-resident adults expected to move off-reef per year. This proportion was translated to emigration by multiplying by the number of adults on a given reef in each year, and was translated to immigration by multiplying by the average per-reef abundance of adults on all reefs in that year ($AI:ix$). Hence, when fishing reduces population size on a reef it is expected that immigration will outweigh emigration, but in the absence of fishing on a reef, net migration should be off-reef because the abundance of adults on that reef will be greater than the average of all (fished and unfished) reefs. Seasonal migrations, such as those that might be associated with aggregating to spawn, were not considered since: i) available information suggests that such movements are temporary and do not result in net immigration or emigration from reefs (Davies 1994, Samoily pers. com.); and ii) sampling during the experiment would be structured to account for or avoid periods of seasonal migrations.

Management and Experimental Treatments

Experimental treatments were imposed by varying the mean value for fishing mortality applied to reefs nominated for each treatment. Thus, for closed reefs, fishing pressure was usually set to zero. For reefs subject to increased fishing pressure, we simply multiplied the ambient average fishing mortality (0.17) by a factor corresponding to how much additional pressure we thought could be applied by us with the cooperation of the fishing fleet(s). We considered we could (deliberately) impose at least as much additional fishing pressure as that which now occurs, and possibly additional pressure up to twice ambient fishing levels. Hence, the average rate of fishing mortality was multiplied by 2 or 3 for those experimental treatments involving increased fishing. Since the mortality factors were applied independently to each reef in each iteration, we could vary the average fishing pressure from year to year to mimic the consequences of, for example, pulse-fishing and reef closure. As with background fishing mortality, we applied stochastic variation in the experimental fishing pressure to account for effects such as bad weather, market fluctuation, and variation in fleet dynamics on the amount of experimental fishing pressure realised. We did not vary fishing pressure seasonally or model explicitly any decline in harvest rate as a result of stock reduction within years because all treatments were expected to apply for at least one year, which would include seasonality in catchability or fishing effort. The fishing mortalities we applied thus represented the net annual rates.

age 3 in our simulations.

We also considered the possibility that reef closures via the GBRMPA zoning plans were not effective. There is considerable anecdotal and circumstantial evidence that infringements of closed reefs are commonplace. We modelled such infringements by setting a parameter called ‘closure effectiveness’, which took values from 1 (closure completely effective, no fishing mortality) to 0 (closure a complete failure, fishing pressure on closed reefs the same as that on all other reefs). Closure effectiveness was expressed in the simulations as the multiplier ‘1-Closure Effectiveness’ applied to line fishing harvest rate, and could be set separately for historical iterations (prior to the commencement of the experiment) and future iterations, simulating closure effectiveness during the experiment.

Sampling Variation

The products of the above simulations were the numbers of recruits, juveniles, and adults on each experimental reef in each year of the experimental work (iterations 31-36). These numbers reflected the effects of population dynamic processes, and variations in them, but did not include the additional variation in field data that would arise because abundances would be estimated from some (sub-) sampling scheme within each reef and would, therefore, inject sampling variation into the perceived variation among reefs and years. We estimated that sampling variation from field data and expressed it as a proportion of the mean (estimated) abundances from those field data (below). This ratio ($\frac{s}{\bar{x}}$) was then used together with a random normal deviate to impose sampling variation on the numbers resulting from the population dynamic models ($A1:xi$). The data analysed, therefore, included the expected effects of sampling variation.

Since the experimental units in the proposed experimental designs were whole reefs, and each reef would be represented in a given analysis by its estimated mean abundance of (*e.g.*) adult coral trout, the sampling variation was in the estimated mean. Derivation of the sampling variation, therefore, depended on the number of (sub)samples from which each mean was derived. Increasing sub-sampling would reduce the expected uncertainty in the estimated mean for each reef. For the purposes of our simulations, we examined only inter-annual changes in abundances on reefs, without references to potential ‘seasonal’ variation, and so our effective sub-sample sizes reflected the total number of sampling days per year. Prior data (Ayling & Ayling 1994, Mapstone & Ayling, unpublished data) indicated that the total number of visual counts feasible per day was 24-30, whilst Davies (1993, 1994) found that up

to 80 fishing 'hangs'[⌘] per day could be realised by a team of 4 dory-men. Since we expected to sample each reef routinely on 1-2 days each year, by either fishing or visual surveys, we incorporated sampling variation arising from sub-samples of 24-60 data/reef.

Monte-Carlo Simulations

We conducted a large number of simulations, using the modified REEF programme, to generate realistic data for analysis by the simplest statistical procedures expected to be applied in the proposed experiment. To examine the statistical properties of each potential experimental design we:

- i. set parameters for the various sources of variation (recruitment, mortality, sampling) and fishing effects (as described above and in Appendix 1);
- ii. ran the simulation 100-200 times independently with each set of parameters;
- iii. tallied the number of times a null hypothesis of zero effect would have been rejected against the relevant significance criterion.

These counts provided a crude empirical measure of the likely statistical power of field data to detect the set fishing effects with the design being simulated.

From the above discussion, it can be seen that the following parameters have to be set for each run:

- ?? Larval supply capacity;
- ?? Proportion of larvae retained or returning to natal reef;
- ?? Scaling applied to background larval supply to clusters;
- ?? Mean inter-annual variation in larval supply;
- ?? Stochastic variation in larval supply among clusters;
- ?? Recruitment capacity (to the demersal population);
- ?? Scaling applied to recruitment on reefs within clusters;
- ?? Within-year similarity in recruitment among clusters;
- ?? Within-year similarity in recruitment among reefs within clusters;
- ?? Level of migration among reefs;

[⌘] A 'hang' is a unit of fishing effort by one fisherman, and represents fishing whilst moored at a fishing location.

- ?? Amount of variation in natural mortality;
- ?? Existing level of fishing mortality;
- ?? Amount of variation in fishing pressure;
- ?? Proportion of population vulnerable to line fishing;
- ?? Fishing pressure imposed by experimental treatment;
- ?? Estimated sampling variation;
- ?? Effectiveness of closure regulations.

If only two values for each of these parameters were considered, $2^8 = 262144$ scenarios could be modelled. In order to reduce this scope to manageable realms, we adopted the following sequential strategy:

- i. assess the need to deliberately impose added fishing pressure to experimental reefs;
- ii. examine the implications of reef and cluster similarity and scaling;
- iii. examine the implications of four hypotheses about the importance of recruitment and settlement processes for subsequent population size;
- iv. examine the effects of increasing stochastic variation in recruitment and mortality, at all scales (simultaneously);
- v. assess the merits of experiments of different designs, especially involving increasing spatial extent (# clusters) versus reduced replication (# reefs) within clusters.

At each of these steps, we maintained all parameters not under consideration constant, to measure the effects of variations in the target parameters alone. For steps i-iv, we included only what we considered the reasonable extreme values (best and worst cases expected in reality) for each of the parameters being evaluated, whilst for case v. we considered experimental design options that seemed logistically and financially feasible but still relevant to the objectives of the study. The default and alternative (trialed) values for all parameters are given in Table 2. These values were used in all simulations except where otherwise stated.

Table 2: Process parameters used in simulations. ‘Default’ values are those used by default in all simulations, unless specified otherwise. The ‘Low’ & ‘High’ values are the values specified when examining the robustness of the data to variations in each parameter.

PARAMETER	Symbol [?]	Values		
		Default	Low	High
Larval supply carrying capacity	k	100.0	5.0	100.0
Larval retention probability	ss	0.05	0.1	0.2
Cluster Scaling of larval supply [⚡]	c_j	3	1	3
Variation in larval supply* :				
- Mean inter-annual	VG	0.63	0.42	0.63
- Among clusters	? _{VGc}	0.28	0.19	0.28
- Among reefs	? _{VG_R}	0.28	0.19	0.28
Recruitment carrying capacity	k'	1000.0	50.0	1000.0
Reef scaling of recruitment capacity [⚡]	r_{ij}	3	1	3
Recruitment similarity within years:				
- Among Clusters	-	0	0	1
- Among Reefs	-	0	0	1
Mean natural survival:				
- settlement to 1 yo	s_o	0.40	-	-
- 1-2yo	$s_{ay,ij}, (a=1)$	0.60	-	-
- 2-3yo	$s_{ay,ij}, (a=2)$	0.70	-	-
- adults	$s_{Ay,ij}$	0.83	-	-
Variation in natural survival*	? _{sa}	0.05	0.03	0.05
Adult migration rate	d_y	0.0	0.1	0.2
Ambient line fishing mortality	$H_{y,ij}$	0.17	0.085	0.17
Variation in fishing mortality*	? _H	0.25	0.16	0.25
Size of fishing pulse	-	3.0	2.0	3.0
Vulnerability to fishing	$P_{y,ij}$	0.95	0.50	0.75
Sampling variation*	? _{obs}	0.20	0.20	0.32
Closure effectiveness	-	1.0	0.50	0.75

[?] Symbolic representation in Appendix 1.

[⚡] Background larval loading scaled among clusters

* Expressed as standard deviation (of the estimator) / mean (?_̄/ \bar{x})

[⚡] Recruitment carrying capacity scaled among reefs

Where possible, the range of values examined for the above parameters reflected the estimates of variation we saw in existing field data. Where relevant data were not available, we chose values arbitrarily with the intention of depicting extreme results. We ran the population dynamics model without any treatment effects under several 'null' scenarios of recruitment variation and inter-reef movement by coral trout to verify that the model produced the expected population behaviour before we trialed experimental designs. Experimental fishing treatments were then imposed by simply altering the rates of fishing mortality for individual reefs.

Necessity of Imposed Fishing Pressure

We discussed three manipulative treatments above:

- Simple Closure (Open ? Closed)
- Open-Pulse-Closure (Open ? Pulse fished for 1 year ? Closed)
- Closed-Pulse-Closure (Closed ? Pulse fished for 1 year ? Closed)

We considered it likely, however, that only one or two of these could be implemented in practice, mainly because of constraints on the numbers of reefs that could be closed to fishing. Clearly, it would be expected that the capacity to recognise differences between fished and unfished reefs and to track changes in the populations on fished reefs after closure would improve with increasing levels of fishing. There would be considerable merit, therefore, in deliberately forcing the reduction of stocks by pulse-fishing, but that benefit would come at considerable financial and logistic cost. In order to estimate the magnitude of benefit of deliberate stock reductions in the context of inherent variations expected of field data, we ran simulations of the first two treatments and the control condition (Closed historically ? remain Closed) imposed at two clusters of reefs, with each treatment replicated within clusters ($n=2$) (Table 3).

Table 3: Treatment regimes for assessing the need to impose additional fishing on experimental reefs. The tabulated numbers are the multiples of mean ambient line fishing mortality ($\bar{H}=0.17pa$) applied to reefs in each treatment in each year. Stochastic variation in fishing mortality ($0.25\bar{H}$) was applied independently to each reef in each year.

TREATMENT	YEAR					
	Past	1995-6	1996-7	1997-8	1998-9	1999-00
Control	0	0	0	0	0	0
Closure	1	0	0	0	0	0
Pulse Fishing	1	3	0	0	0	0

The size of the experimental fishing pulse was set to three times the average natural fishing mortality - *i.e.* we expected that it would be possible to impose experimental fishing locally equivalent to about twice the ambient fishing pressure, resulting in a total fishing pressure on experimental reefs of three times existing levels.

We also considered the implications of imposing the pulsed fishing treatments on replicate reefs in successive years, rather than all reefs being pulse-fished in the same year. This was considered a desirable strategy to avoid the potential for our experimental results to be affected unduly by events (*e.g.* recruitment) related to or following a single year. For example, if recruitment was very high in the year following pulse-fishing, the relevance of the results of the experiment to years of lower recruitment may be questioned. Clearly the imposition of ‘staggered starts’ also has costs and benefits. The costs are i) replication of the pulse fishing treatment in each cluster within any one year is reduced, possibly eliminated ($n=1$); and ii) the power to measure responses to closure over years after pulse-fishing probably will be decreased because inter-replicate variance will include the effects of interactions between treatments and inter-annual variations in recruitment. The benefits include: i) reduced risk of the results being affected by an unfortunate choice of the year to do the pulse-fishing; and ii) greater generality (but less certainty) of statements about the dynamics of exploited populations during heavy fishing or following protection from fishing. To compare the statistical properties of the two options, we compared the power of simulation data to detect the difference between control reefs and pulse-fished reefs in which all fishing occurred in one year with the analogous statistic derived when pulse-fishing was applied over two years at each cluster, with different replicate reefs being treated in each year.

Sensitivity to variation in recruitment

Inter-reef variation in recruitment would affect the potential to extract useful signals from the noisy data expected of the proposed experiment. We discussed above (and in Appendix 1) how we introduced into the model reef-scale and cluster-scale variation in larval supply and recruitment. We ran simulations varying the parameters for carrying capacity of larvae and recruits, cluster- and reef-similarity within years, and cluster- and reef-scale scaling in (respectively) larval supply and recruitment to cover a wide range of possible levels of ‘nuisance’ variation. The experimental design for these trials was 2 clusters of 6 reefs, with 2 reefs closed to fishing, and 2 reefs pulse fished and then closed in each of two successive years. The choice of design here was arbitrary because the relative effects of different scenarios of recruitment variation would be consistent across different experimental designs.

The two capacity parameters were combined to provide four scenarios of larval supply and recruitment, defined as follows:

Scenario 1 :	larval supply k=5.0	recruitment k=50.0
Scenario 2 :	larval supply k=5.0	recruitment k=1000.0
Scenario 3 :	larval supply k=100.0	recruitment k=50.0
Scenario 4 :	larval supply k=100.0	recruitment k=1000.0

These scenarios reflect four hypotheses about the larval supply and settlement processes driving populations of fish on reefs:

H₁: Larval supply ~independent of spawning stock, but recruitment limited by reef populations.

H₂: Larval supply ~independent of spawning stock, and recruitment limited by larval supply.

H₃: Larval supply ~proportional to spawning stock, and recruitment limited by reef populations

H₄: Larval supply ~proportional to spawning stock, and recruitment limited by larval supply.

The four parameters controlling reef- and cluster-specific variation (cluster- and reef-scaling, cluster- and reef-similarity) were each assigned the ‘high’ or ‘low’ values in Table 2 and varied orthogonally to give a total of sixteen scenarios for the spatio-temporal variability in the simulation data. One hundred (100) simulations were carried out for each variation scenario

and for each of the above four ‘larval supply - recruitment’ hypotheses (giving a total of 64 cases). The number of significantly non-zero effects detected in the data from these 64 cases were then analysed by a separate GLM procedure to determine the influence of each of the four hypotheses and four variability parameters.

We also varied the amount of larval self-seeding for each reef and the amount of adult inter-reef migration, but for only one of the above 64 cases (the most variable). These trials were done with an experimental design of 6 clusters of 4 reefs with two treatments (Closed-Closed, Open-Pulsed-Closed), with the pulse fishing being applied to one reef per cluster in each of two successive years. The pulse fishing level increased fishing mortality to three times existing ambient mean harvest rate.

Sensitivity to management and fishing parameters

For the most variable of the above 64 cases (reefs and clusters dissimilar within years and three-fold scaling at both scales; larval-recruitment scenario 4), we assessed the robustness of the simulation data to changes in some of the management and fishing parameters. We varied the effectiveness of reef closure, the proportion of target populations vulnerable to fishing, the base line fishing mortality, and the size of the experimental reduction in stock size. Each of the variations was introduced one at a time, applying alternately the ‘Low’ and ‘High’ parameter values given in Table 2, with 200 simulations of each case.

Effects of experimental design

Finally, we compared the power to detect annual contrasts between fishing and control treatments for each of the experimental designs identified in Table 1. Each of the designs included some or all of the treatments depicted in Table 4.

Table 4: Experimental treatment structure expressed in terms of the amount of fishing expected on reefs in each of the preferred treatments. The tabulated numbers indicate the amount of line fishing applied to reefs relative to the expected average ambient fishing pressure ($\bar{H} = 0.17$).

TREATMENT	YEAR					
	1: Past	2: 1995- 6	3: 1996- 7	4: 1997- 8	5: 1998- 9	6: 1999- 00
Control	0	0	0	0	0	0
Open-Pulse Y ₂	1	3	0	0	0	0
Open-Pulse Y ₃	1	1	3	0	0	0
Open-Pulse Y ₅	1	1	1	1	3	0

Closed-Pulse Y₂	0	3	0	0	0	0
Closed-Pulse Y₄	0	0	0	3	0	0

‘Best’ and ‘Worst’ case scenarios were defined for each experimental design and we ran 200 simulations of each. ‘Best’ and ‘Worst’ case scenarios were depicted by varying the several ‘non-experimental’ parameters, whilst maintaining all others at their default values. The characteristics of ‘Best’ and ‘Worst’ cases are given in Table 5 (below), whilst the default values for all parameters are given in Table 2.

Table 5: Parameters and their values used to define ‘Best’ and ‘Worst’ case scenarios of nuisance variation for the assessment of different experimental designs.

PARAMETER	CASE	
	Best	Worst
Larval/settlement scenario	4	4
Similarity within years:		
- Among Clusters	1	0
- Among Reefs	1	0
Scaling among clusters	1	3
Scaling within clusters	1	3
Adult migration rate	0.0	0.1
Closure effectiveness (History)	1.0	0.5
Closure effectiveness (Future)	1.0	0.5

Analyses of Simulation Data

The simulated data produced from the model were analysed by two methods: i) Analyses of Variance (ANOVA) involving annually repeated measures on each reef, in which corrections for autocorrelation among the repeated measurements were calculated and F-tests done on the assumption of a standard F-distribution; and ii) the estimation of annual treatment-control contrasts between residual values after fitting a simplified General Linear Model to the simulated data. In each case, the 100 or 200 simulations of each scenario were analysed independently by one or more of these methods, and the number of statistically significant effects of interest were tallied. These tallies provided estimates of the power of the analyses to detect departures from zero treatment effects, given the modelled sources of variation. No *a-posteriori* estimation of the magnitudes of significantly non-zero effects were examined. Details of these analyses are provided in Appendix 2.

Existing Information & Demographic Parameters for Simulation Models

There has been considerable improvement in our understanding of the demographics of some of the species targeted by the reef line/spear fishery since Walters' and Sainsbury's work in 1990. Wherever possible, we used estimates of demographic parameters (survivorship, migration, recruitment variation, *etc.*) from recent research on coral trout to tune the models so that the resultant population dynamics resembled what we know of those on the GBR.ⁱ We also derived estimates of coefficients of variation for the *estimators* (? sample SE/mean), and those ratios were used to generate the stochastic variation expected of respective parameters.

Variation in Larval Supply & Recruitment

Estimates of inter-annual and inter-reef variation in recruitment were derived from work by P.J. Doherty (AIMS), M. Samoily's (QDPI), and A.M. & A.L. Ayling (Sea Research). Replicate visual counts of recruit *P. leopardus* were available from Green Island and Arlington Reef over 34 years (Doherty & Samoily's) and from 47 reefs off Townsville-Ingham over 2-3 years (Ayling & Ayling). These data were used as follows:

- i. mean recruitment was calculated for each reef in each year;
- ii. standard deviation among those yearly means was calculated for each reef;
- iii. the ratio of that inter-annual SD of the means to the mean over all years was calculated for each reef.

The average of these CVs over all reefs within a data set was then taken as the best (point) estimate of relative inter-annual variation in recruitment. The average inter-annual CVs from Doherty's & Samoily's' data and Ayling's & Ayling's data were 0.72 and 0.70 respectively. We were able to partition estimated sampling variation out of these gross estimates for the Ayling & Ayling data we had, but not for the other data. Removing sampling variation reduced the average CV to 0.63. This ratio generated a 13-15 fold inter-annual range in recruitment.

Note that 'recruitment' in our simulations was defined as appearance at the end of the first year post-settlement, whereas the estimates of recruitment from Doherty, Samoily's, & Ayling & Ayling were from counts of fish estimated to be less than 6 months post-settlement, and

often less than 34 months post settlement. We chose, therefore, to apply the empirical estimates of variation in ‘recruitment’ to modelled larval supply, rather than what we defined as recruitment. We used the above value of 0.63 for mean inter-annual CV as our default value. Estimated inter-reef standard deviation of the (mean) inter-annual CV was 0.28, which was the default value we used to provide stochastic spatial variation in recruitment among a) reefs, and b) clusters within years.

Mortality

Estimates of total mortality for coral trout (mostly *P. leopardus*) were obtained from a FR&DC report resulting from collaborative work by JCU (G. Russ, B. Ferreira), QDPI (I. Brown, M. Samoilys, G. McPherson), and AIMS (D. Williams, P. Doherty) (Brown 1994). Eleven independent estimates of total mortality were derived from 9 reefs, mostly in the Townsville-Innisfail region. Three estimates were derived for Lizard Island, two of which were from areas closed to fishing. All estimates were for the composite population of fish over 2 or 3 years of age. We assumed that fishing occurred on all the reefs from which the estimates came (including reefs notionally closed to fishing), but that fishing at Lizard Island was likely to have been less than elsewhere, at least in those areas closed to fishing.

Natural Mortality

We took the average of the Lizard Island estimates of mortality to be an upper estimate of natural mortality. We made this assumption because:

- i. The Lizard Island estimates were the lowest of all estimates, and anecdotal evidence suggested that fishing mortality around Lizard Island has been very low, particularly in the closed areas.
- ii. The distance of Lizard Island from population centres was likely to mean relatively low levels of recreational fishing;
- iii. The presence of a resort and research station on Lizard Island, with relatively high visitation by tourists and researchers, would make infringements of closures at Lizard Island conspicuous, and therefore unlikely; and
- iv. Anecdotal information that many commercial line fishers do not fish at Lizard because of the high profile of other users there.

ⁱ Results from much of this work were available to us, though not yet in press, and we are grateful to several researchers for access to their unpublished data.

The mean point estimate of mortality from Lizard Reef was 0.17pa, which we adopted as the best available estimate of natural mortality for adult *P. leopardus*. Given that at least some fishing occurs on Lizard Reef, this is likely to be an over-estimate of natural mortality for the population targeted by the legal fisheries.

We have no field estimates of mortality of coral trout before they enter the fishery. To derive mortality parameters for the two years between what we defined as recruitment and the adult populations, we assumed that:

- i. mortality decreased with age/size during these juvenile years, with juvenile mortality declining by about 33% per year;
- ii. the maximum ages recorded from Lizard Reef and all other reefs reflected expected longevity for unfished and fished stocks respectively;
- iii. mortality should be applied to the modelled juvenile age classes such that the relative strengths of cohorts at those maximum ages in modelled populations under fished and unfished scenarios should approximate those observed in the field.

Accordingly, we derived estimated rates of mortality for juvenile cohorts (by iteration) to be 0.6, 0.4, 0.27 (rounded to 0.3) for the first, second and third years post-settlement.

Variation in natural mortality was derived from variation in estimates of mortality from of Lizard Island (default $\bar{x} = 0.05 \bar{x}$).

Fishing Mortality

We derived estimates of fishing mortality for other open or closed reefs by subtracting the mean value of (natural) mortality for Lizard reef from the means for all other open or closed reefs respectively. Our point estimates of fishing mortality were 0.14 for open reefs and 0.20 for closed reefs(!), with a weighted average rate of 0.163. Given that it was likely that our estimates of natural mortality from Lizard Reef was too high, the estimates of fishing mortality on open reefs were probably under-estimates, although we do not know by how much. The higher estimate of fishing mortality from closed reefs should be considered with caution, and may have arisen because different methods of estimating total mortality were used for those

reefs than for all other reefs (including Lizard Island) and because of the dominance of a single year-class in populations on the closed reefs (Brown 1994).

We derived a second independent estimate of fishing mortality by analysing the rates of public tag-returns from *P. leopardus* tagged on reefs off Innisfail by C. Davies between 1992 and 1994. The average estimated fishing mortality was 0.119pa and 0.128pa for (assumed) natural mortality of 0.15 and 0.20 respectively. The estimated fishing mortality for the closed reef in the group studied by Davies was 0.043-0.047pa.

These estimates were expected to be under-estimates because of non-fishing tag-losses (which may be high, Davies pers. comm.), and failure by some fishers to return tags. Thus, we considered that existing average fishing mortality (\bar{H}) was between about 12% and 20% per annum and we set the average rate to 17% in our models. Variation in fishing mortality was estimated by variation in estimated fishing mortality across all reefs other than Lizard Island. Estimated $CV_{\bar{H}}$ was 0.30 for the FR&DC data and 0.13 for Davies' tag-return data. We set the default value for simulations at 0.25.

Inter-reef movement

Walters and Sainsbury (1990) emphasised that low rates of inter-reef migration of adult fish subject to experimental investigations would be critical to the success of treating individual reefs as replicate experimental units. Davies (1993, 1994) has investigated by tag-release-recapture studies inter-reef movements by several species, with particular emphasis on *P. leopardus*. He tagged over 4,500 *P. leopardus* on 5 neighbouring reefs off Innisfail, north of Townsville. In four research cruises where recaptures of tagged fish were possible, 142 tagged *P. leopardus* were recaptured, but only one fish had moved between reefs since release. That fish had moved only several hundred metres between two close adjacent reefs (Beaver & Taylor Reefs). All other fish were recovered from the same reef on which they had been tagged and released. The release-recapture intervals ranged between 6 and 22 months.

During the same period, the fishing public returned 323 tags from Davies' study. Taken at face value, and ignoring all returns of tags released on Beaver Reef (which was notionally closed to fishing), these data indicated emigration rates of -6%, -26%, -29%, and -33% from Farquharson, Taylor, 17060/61, and Potter Reefs respectively. Rates of immigration to the

same reefs were 20%, 26%, 33%, & 22% respectively, giving net migration rates of 14%, 0%, 4%, & -11% respectively.

We are unable to explain categorically the discrepancies between migration rates indicated by research and public tag returns, but several factors lead us to believe that the research returns are likely to be the best indicators of true migration rates:

- i. We know from discussion with some of the people who returned tags that there was some uncertainty and/or inaccuracy about the names of the reefs on which they had been fishing, or on which of several reefs visited during a fishing trip the tagged fish were caught;
- ii. the research cruises were timed to highlight movements of *P. leopardus* associated with spawning, with one trip each year during spawning and one trip off the spawning period, and it was expected that most movement might occur before or after aggregating to spawn;
- iii. sampling on the last research trip was targeted at those areas and reefs where most migration had been suggested from public returns - specifically the nearest-neighbouring regions of Potter and 17060/61 and of Beaver and Taylor Reefs.

Despite sampling on research trips to maximise the estimates of inter-reef movement, virtually none was recorded.

In modelling potential experimental scenarios, therefore, we initially set inter-reef migration to zero. We considered the implications for the preferred design options, however, of inter-reef exchange of post-settlement *P. leopardus* of 10% and 20% per annum.

Inter-reef & inter-cluster variation in estimated abundance.

Estimates of variations in abundances of some fish species (including *P. leopardus*) were derived from visual survey data from the Cairns section of the GBRMP collected in 1989-90 (24 reefs) and 1990-91 (50 reefs) (Mapstone & Ayling unpublished data), and four reefs off Townsville (1983-94 - Ayling & Ayling 1993, 1994). Within-reef variation and sampling variation were estimated from hierarchical ANOVA models and removed from estimated variation among reef means, resulting in estimates of variation among reefs alone. Population densities of coral trout on reefs in close proximity (1,000-10,000m) varied by 1.5 fold on

average, whilst abundances varied by up to 3-fold regionally (among 'clusters'). These measures provided reference points against which to tune the population dynamics models such that they produced simulated populations consistent with field data.

Sampling Variation

Sampling variation within reefs was estimated from the above mentioned visual survey data and from CPUE data from Davies' work (Davies 1993, 1994). SE/mean values for CPUE data at a whole-reef scale were generally below 0.2, whilst SE/mean values for visual surveys varied between 0.32 and 0.22, depending on the amount of sampling effort per reef. Note that the values for CV_{mean} for visual survey data were calculated from the estimated Mean Square within reefs, and so represented the sum of all scale-related variation within reefs estimable from the available data. They thus reflected the uncertainty in reef-means expected of field data. We varied sampling variation by applying CV_{mean} ratios of 0.2 and 0.32, according to expected sampling intensity (60 & 24 samples per reef respectively), to examine the effects of increased sampling variation on measurements of the effects of experimental fishing on densities of coral trout.

Trawling mortality

Although it is beyond the brief (and budget) of the CRC to consider the effects of trawling as part of the proposed experiments, we have considered the potential to facilitate future experiments of the type considered by Walters and Sainsbury (1990) in response to a request from CSIRO (Cleveland) and QDPI. If the work we commence were to be extended in future to encompass experimental trawling on some clusters, we would need to consider the consequences for the line fishing work of effects on *P. leopardus* caused by inter-reef trawling. Estimates of the potential for trawlers to catch *P. leopardus* were derived from data from the project being done by CSIRO and QDPI on the environmental effects of prawn trawling in the Far North Section of the GBR Marine Park. In trawling 88 stations with modified Frank & Bryce gear, few coral trout (of any species) were caught, and none were *P. leopardus*. We considered these data to indicate negligible potential for direct trawl-induced mortality of *P. leopardus*. Walters and Sainsbury (1990) suggested that inter-reef trawling may principally affect coral trout by reducing inter-reef migration (see Appendix 1, ix). Since such an effect would enhance our capacity to detect effects of line fishing treatments, we have not modelled those effects explicitly, other than by varying rates of inter-reef migration. We assumed that any trawl-mediated effects (on migration) would affect all reefs equally.

RESULTS OF SIMULATIONS

Necessity of Imposed Fishing Pressure

The statistical power to detect contrasts between control (closed) and treatment reefs in each year are given for both 'open and then closed' only, and 'open, pulse fished and closed' treatments in Table 6. The contrasts were analysed by both simplified GLM and full-model Repeated Measures Analysis of Variance (RMANOVA) following correction for autocorrelation (Appendix 2). The imposition of additional fishing pressure prior to closure increased the potential to recognise effects of fishing by almost two-fold over the subsequent life of the experiment. Thus, the potential to recognise differences in the transient responses of populations protected from fishing would be enhanced considerably by additional (deliberate) fishing, even when considerable nuisance variation was present. Clearly, the degree of improvement gained will depend on the amount of additional fishing imposed during the pulse year. The effect of failing to achieve the 3-fold increase in fishing pressure considered here is examined later (Table 9).

The GLM procedure appeared consistently more powerful than the full-model ANOVA in these and all other analyses (Tables 6-11). The GLM analysis incorporated into the REEF model used a simplified model (compared with the ANOVA) to construct the contrasts within years, with the result that the degrees of freedom for the GLM tests were greater than those in the ANOVA framework. The apparent advantage of the GLM procedure is gained, however, on the basis of additional assumptions about the presence or absence of some interactions in the field data (Appendix 2, Walters & Sainsbury 1990). These assumptions seem legitimate in our simulation data, but should be examined explicitly as real field data become available because we did not explicitly precipitate such interactions in our simulation output.

Table 6: Comparison of expected statistical power to detect annual differences between historically closed and experimentally closed reefs in the presence and absence of additional (to ambient) fishing prior to closure. Both RMANOVA and GLM results are given for a design incorporating 2 clusters each of 6 reefs, with each of the three treatments (control, closed, pulsed & closed) applied to two reefs per cluster. A ‘high variation’ scenario was assumed, with reefs and clusters acting independently, with 3-fold scaling of larval supply (between clusters) and recruitment capacity (among reefs), and population hypothesis 4 (above). Total fishing pressure during the pulse was on average 3 times ambient fishing, and sampling intensity was 60 samples per reef per year. Shown in the lower section of the table are the results of staggering the application of treatments, with one replicate reef being closed or fished & closed in each of two successive years.

TREATMENT	Analysis	Baseline	Closure Pulse	YEAR			
				C P+1	C P+2	C P+3	C P+4
Open? Closed	GLM	0.63	0.47	0.36	0.29	0.23	0.20
Pulse? Closed		0.60	0.87	0.73	0.57	0.42	0.32
Open? Closed	ANOVA	0.48	0.33	0.25	0.20	0.16	0.14
Pulse? Closed		0.47	0.74	0.56	0.41	0.30	0.22
				STAGGERED		STARTS	
Pulse? Closed	GLM	0.63	0.95	0.87	0.74	0.56	0.52
	ANOVA	0.25	0.59	0.43	0.26	0.22	0.17

Sensitivity to variation in recruitment & inter-reef movement

Power to detect treatment-control contrasts varied significantly with changes in most parameters controlling variations in larval supply and recruitment (Table 7). The sizes of the effects on power, however, were small in most instances. As expected, increasing dissimilarity in recruitment among reefs within years, and increasing scaling in larval supply (among clusters) and recruitment capacity all reduced the power of the simulated experiments to recognise the imposed treatment effects. Hypothesis 4 (the default) has the lowest power in most cases since larval supply is not limited (by carrying capacity) and variability in the larval supply is least ‘damped’ when recruitment is relatively independent of existing population (or recruitment) density. Note that the influence of each of the sources of additional variation is amplified over the recovery phase, as the magnitude of the treatment-control contrast declines and the uncertainty of its recognition increases.

Table 7: Influence on expected power of GLM treatment-control contrasts of changing magnitudes and/or character of different sources of variation, and different larval supply-recruitment limitation hypotheses. The experimental design was one of 2 clusters of six reefs, with 60 data/reef. The default scenario had reef and cluster scale variations similar within years, a three-fold scaling of both larval supply (among clusters) and recruitment capacity (among reefs), and recruitment independent of density following unlimited larval supply (Larval-recruitment hypothesis 4). The power for this case is given in the column headed **Default**. All other numbers are the differences from this base case when one of the forms of variation is turned on or off, as indicated in column headings. Only the main effect results are shown, and all significant differences in power are in bold type (Critical Type I error rate= 0.05).

Year	Params. Default	Similarity		Scaling		Hypothesis			
		Reef=0	Clust.= 0	Reef=1	Clust.= 1	H1	H2	H3	H4
Base	0.95	-0.023	-0.009	0.021	0.010	0.02 1	0.004	0.01 6	0
Pulse	1.00	0.001	-0.007	0.002	-0.002	0.003	- 0.00 5	0.00 5	0
P+1	0.98	-0.013	-0.002	0.015	-0.003	0.00 8	-0.007	0.01 2	0
P+2	0.93	-0.063	-0.016	0.030	0.020	0.02 3	0.008	0.03 1	0
P+3	0.82	-0.12	-0.002	0.045	0.029	0.03 7	0.04 1	0.020	0
P+4	0.46	-0.10	-0.002	0.046	0.052	0.03 6	0.08 1	0.018	0

The effects of inter-reef migration (assumed to be zero in most cases) and a high degree of local self-seeding on the results of proposed experiments are given in Table 8. Increasing local recruitment would be expected to translate the effects of stock reduction through fishing into declines in recruitment, because of the stronger dependence of recruitment on local spawning stock size. This effectively perpetuates the contrast between treatment and control reefs, with treatment reefs taking longer (on average) to recover from stock reduction than when recruitment is unrelated to the local stock. Hence, the power to detect transient differences between control and treatment reefs is slightly greater than in the default case in all years. Such an effect might be expected also if fishing pressure over much of the GBR increased concurrently with the proposed experiment, irrespective of the degree of local self-seeding.

As found by Walters & Sainsbury (1990), increasing inter-reef migration effectively dilutes the effects of reef-scale manipulations of stock size by fishing. Migration rates of up to about

10% per annum caused a decrease in the power to detect a contrast by around 10% in the year following pulse fishing, but this increased to a 50% reduction in power after 4 years. Whilst these results are probably acceptable, migration of 20%pa would mean that the experiment would yield productive information for only about 2 years post-manipulation, after which the treatment and control reefs would be almost indistinguishable (Table 8).

Table 8: Expected statistical power (by GLM) to detect contrasts between treatment and control reefs in each year, when inter-reef migration of adults or local self-seeding were greater than expected. The ‘Base Results’ are those obtained when self-seeding was 0.05 and adult migration was zero, with all other population parameters and parameters governing stochastic variation set at their default values (Table 2). The experimental design in these trials involved 6 clusters of 4 reefs, with 2 control and 2 treatment reefs per cluster, pulse fishing applied in successive years, and 24 sub-samples per reef per year.

PARAMETER	Base Values	Alternative Values	YEAR					
			B’line	Pulse	P+1	P+2	P+3	P+4
Base Results			0.95	1.00	0.98	0.88	0.71	0.29
Adult Migration	0.0	0.10	0.85	0.99	0.89	0.64	0.36	0.14
		0.20	0.64	0.97	0.70	0.36	0.15	0.10
Self-Seeding	0.05	0.10	0.95	1.00	0.99	0.89	0.75	0.33
		0.20	0.96	1.00	0.99	0.91	0.82	0.38

Sensitivity to management and fishing parameters

The results of simulations in which various modelled fishing and closure parameters were varied are shown in Table 9. In all cases, the effects of ‘undermining’ factors such as ineffectiveness of reef closures, failure to impose the expected amount of experimental fishing, etc, are relatively slight in the year of stock reduction through pulse-fishing. Effectively, it seems that the magnitude of reduction planned, even if pulse-fishing is only half as effective as expected, is sufficient to create a strong signal in the abundance measures, despite high nuisance variation. The main concerns arise when:

- i. fishing mortality is considerably less than expected (power drops from 1.0 to 0.82);
- ii. regulatory closures to fishing are grossly ineffective (power ? 0.90); and
- iii. a large fraction of the adult stock is unavailable to the fishery (power ? 0.86).

We have no substantive evidence about the likelihood of these possibilities, though we expect our estimates of fishing mortality to be under-estimates (see above), and we have (anecdotal) reason to believe that infringements of reef closures is commonplace. Indeed, the tag-return data from Davies (1993, 1994) indicated fishing mortality from a single closed reef (Beaver reef) to be about 50% of that on 4 nearby open reefs. Even in this case, the expected power of the modelled experiments was above 0.80. When all the above parameters were set to their ‘worst case’ values at once, however, the expected power of the experiment was

untenable in all years. If such a case was realised, two inferences might be made: i) the experiment would be unproductive; and ii) coral trout would seem to have a high degree of inertia to increased fishing pressure by virtue of their limited availability to the (current) fishery.

Again, however, the consequences of failure of management regimes or inaccuracies in our estimates of fishing pressure, movement etc. increase with time following the pulse-fishing treatment. By the end of the proposed experiment, the power to detect effects of the experimental fishing and closure 3-4 years previously has fallen from the default case by over 50% in some cases. Note that here (and elsewhere) the apparent power to detect contrasts in year P+4 drops markedly. This is mainly an artefact of the staggered treatment of experimental reefs combined with the curtailment of the experiment in 1999-2000. Thus, at the completion of the work there is only a single reef in each cluster that is in its fourth year after closure. The second treatment reef is in only the third year after closure.

Table 9: Expected statistical power (by GLM) to detect contrasts between treatment and control reefs in each year, given failures in management of closed reefs, and erroneous estimates of fishing mortality, stock availability, and the amount of experimental fishing applied to treatment reefs. The ‘Base Results’ are those obtained when all the parameters in the table were set to their default values (Table 2). The experimental design in these trials involved 6 clusters of 4 reefs, with two control and two treatment reefs in each cluster, and pulse fishing applied in successive years. Parameters governing stochastic variation and population dynamic hypotheses were set at their default values (Table 2) for all trials, and we assumed that each reef was sampled with 24 data per year (sampling variation = 0.32).

PARAMETER	Base Values	Alternative Values	YEAR					
			B'line	Pulse	P+1	P+2	P+3	P+4
Base Results			0.95	1.00	0.98	0.88	0.71	0.29
Closure Success	<i>1.00</i>	<i>0.75</i>	0.80	0.98	0.90	0.70	0.50	0.18
		<i>0.50</i>	0.46	0.90	0.72	0.50	0.29	0.14
Vulnerability	<i>0.95</i>	<i>0.75</i>	0.89	0.98	0.94	0.77	0.58	0.21
		<i>0.50</i>	0.68	0.86	0.74	0.55	0.36	0.16
Pulse Effect	<i>3 fold</i>	<i>2 fold</i>	0.94	0.98	0.95	0.77	0.58	0.22
Fishing Mortality	<i>0.17 pa</i>	<i>0.085</i>	0.67	0.82	0.71	0.53	0.35	0.16

All parameters = ‘alternate’ values	0.9	0.13	0.10	0.07	0.08	0.08
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Effects of experimental design

The expected statistical power to detect annual contrasts between treatment and control reefs in different experimental designs are given in Table 10. Clearly, under the ‘Best Case’ scenario, comprising moderate stochastic variation, highly effective closures, and no inter-reef migration of adult fish, all the designs we considered would perform well for up to three years post-manipulation, even if reefs were sampled only once per year ($n=24$). Under these circumstances, there would be no purely statistical reason for discriminating among designs, although clearly other considerations would prioritize some designs over others (see below).

Discrimination among design options was clearer under the ‘Worst Case’ scenarios. The 4-6 cluster designs with local replication of treatments have significantly and substantially better statistical power to detect treatment effects when nuisance variation was large. Only the 20-24 reef designs performed satisfactorily in the year of stock reduction and immediately after if sampled only once per year. The locally unreplicated design (6x2) performed poorly when stochastic variation was high, and none of the designs had acceptable power to follow treatment effects beyond the first year post manipulation under highly variable conditions. The safest strategy to guard against nuisance variations then, was clearly to adopt designs involving at least 24 reefs, whether as 4 clusters of 6 reefs or 6 clusters of 4 reefs. It was also clear that two days sub-sampling per reef per year offered additional security against ‘failure’ of the experiment, where failure here means the production of equivocal results.

Table 10: Comparison of the power (by GLM) of various experimental designs to detect treatment-control contrasts in each year under ‘Best’ and ‘Worst’ case scenarios of nuisance variation. Standard Errors for the tabled figures are approximately ±2%. ‘Replications’ indicate the number of reefs of each ‘treatment’ (table 4) in each cluster. n_s is the number of sub-samples from which reef estimates are derived in each year.

Desig (CxR)	Treatments & Replication	YEAR					
		Baselin	Pulse	P+1	P+2	P+3	P+4
$n_s=60$		BEST CASE[?]					
2x6	2-C, 2-OP _{2,3}	0.99	1.00	1.00	0.96	0.89	0.56
3x4	2-C, 1-OP _{2,3}	0.98	1.00	0.99	0.95	0.87	0.51
6x2	1-C, 1-OP ₂	0.94	1.00	0.95	0.87	0.79	0.65
4x4	2-C, 1-OP _{2,3}	0.99	1.00	1.00	0.97	0.91	0.61
5x4	2-C, 1-OP _{2,3}	1.00	1.00	1.00	0.99	0.97	0.64
6x4	2-C, 1-OP _{2,3}	1.00	1.00	1.00	0.99	0.98	0.80
4x6	2-C, 2-OP _{2,3}	1.00	1.00	1.00	1.00	0.99	0.81
4x6	2-C, 1-OP _{3,5} , 1- - C vs CP	0.18	1.00	0.98	0.93	0.78	0.66
	- C vs OP	1.00	1.00	1.00	0.99	0.97	0.63
$n_s=24$							
2x6	2-C, 2-OP _{2,3}	0.89	0.99	0.94	0.85	0.70	0.34
3x4	2-C, 1-OP _{2,3}	0.90	0.98	0.94	0.77	0.65	0.26
6x2	1-C, 1-OP ₂	0.66	0.93	0.78	0.67	0.48	0.36
4x4	2-C, 1-OP _{2,3}	0.95	1.00	0.98	0.88	0.75	0.35
5x4	2-C, 1-OP _{2,3}	0.99	1.00	0.98	0.94	0.84	0.40
6x4	2-C, 1-OP _{2,3}	0.99	1.00	0.99	0.96	0.85	0.52
4x6	2-C, 2-OP _{2,3}	0.99	1.00	0.99	0.99	0.93	0.58
4x6	2-C, 1-OP _{3,5} , 1- - C vs CP	0.10	0.95	0.79	0.64	0.47	0.37
	- C vs OP	0.95	1.00	0.97	0.89	0.82	0.33
$n_s=60$		WORST CASE[?]					
2x6	2-C, 2-OP _{2,3}	0.31	0.76	0.48	0.30	0.18	0.10
3x4	2-C, 1-OP _{2,3}	0.25	0.79	0.42	0.28	0.13	0.13
6x2	1-C, 1-OP ₂	0.18	0.58	0.30	0.21	0.13	0.12
4x4	2-C, 1-OP _{2,3}	0.34	0.86	0.51	0.36	0.16	0.07
5x4	2-C, 1-OP _{2,3}	0.41	0.93	0.71	0.44	0.30	0.12
6x4	2-C, 1-OP _{2,3}	0.50	0.95	0.76	0.50	0.24	0.10
4x6	2-C, 2-OP _{2,3}	0.42	0.95	0.75	0.45	0.26	0.11
4x6	2-C, 1-OP _{3,5} , 1- - C vs CP	0.07	0.80	0.48	0.28	0.16	0.11
	- C vs OP	0.32	0.90	0.59	0.30	0.21	0.09
$n_s=24$							
2x6	2-C, 2-OP _{2,3}	0.23	0.53	0.31	0.20	0.13	0.09
3x4	2-C, 1-OP _{2,3}	0.19	0.55	0.25	0.16	0.09	0.10
6x2	1-C, 1-OP ₂	0.15	0.39	0.19	0.12	0.10	0.09
4x4	2-C, 1-OP _{2,3}	0.23	0.68	0.25	0.16	0.11	0.07
5x4	2-C, 1-OP _{2,3}	0.27	0.75	0.46	0.28	0.20	0.09
6x4	2-C, 1-OP _{2,3}	0.36	0.84	0.54	0.31	0.15	0.10
4x6	2-C, 2-OP _{2,3}	0.28	0.82	0.56	0.27	0.16	0.09
4x6	2-C, 1-OP _{3,5} , 1- - C vs CP	0.10	0.55	0.30	0.17	0.12	0.09
	- C vs OP	0.21	0.75	0.42	0.20	0.12	0.06

[?] **BEST CASE:** Low recruitment variation, Closure Effectiveness =100%, Adult Migration = 0%

[?] **WORST CASE:** High recruitment variation : Closure Effectiveness =50% : Adult Migration = 10%

DISCUSSION

Our results show that large scale experiments to examine empirically the effects of line fishing on fish stocks and catch rates are likely to be informative even when uncontrollable variation is extreme. We have demonstrated, however, that under the most disruptive regimes of nuisance variation, such experiments will have to be very large (involving at least 20 reefs) to ensure some confidence that the results will be inferentially sound.

The results of the modelling work were presented at a workshop of researchers and managers in July 1994, where discussion focussed on the synthesis of model results with other factors affecting the design and implementation of potential effects of line fishing (ELF) experiments. The scientific basis and need for an experiment of the sort considered was endorsed at that workshop, and in extensive consultation with scientists, fishing sectors, management agencies, and the public since then. These consultations inevitably have influenced the choice of experimental design, and our recommendations. Although much of the discussion of the proposed ELF Experiment focussed on implementation of such an experiment, we do not discuss implementation extensively, which is covered in detail elsewhere, in research proposals for review and an operational plan for the implementation of the experiment in the context of other Effects of Line Fishing tasks.

Preferred Designs

The results of the modelling work indicated that statistically robust and powerful experimental designs were feasible over a range of geographic scales of implementation. Under conditions of high natural variation, however, designs of less than 24 reefs would be unlikely to produce clear 'signals' above the background noise. The choice of design, therefore, tended to be cast more in terms of how wide to spread the 4-6 clusters rather than whether highly localised or widespread designs were preferable. Representatives of the GBRMPA at the July 1994 workshop, and several researchers, argued strongly that it was important to spread the experimental reefs over as large an area as reasonably feasible to maximise the generality of the results to management of the GBR Region. That view has been endorsed subsequently by most interested parties. Further, it was considered important to facilitate as far as possible the later implementation of research into the effects of inter-reef prawn trawling on reef line fisheries. For both issues, it was clearly desirable to maximise the number of clusters at which

line fishing treatments were imposed. It was generally considered unfeasible, however, for work to proceed at more than 6 clusters given current funding of the ELF project.

At the same time, most researchers felt strongly that it was essential to maintain at least some replication of line-fishing treatments within clusters - *i.e.* there should be at least 2 reefs per treatment per cluster. The above modelling results also indicated that locally unreplicated designs were the weakest statistically. It was agreed that sampling at more than 24 reefs would be impossible, and some researchers considered that 24 reefs may prove too difficult. With a constraint of 24 reefs, a desire to spread the work over four-six clusters, and to retain local replication of experimental units (reefs), only 2 or 3 treatments per cluster were feasible. Including more treatments would necessarily involve reducing the geographic scope and/or number of clusters at which the work would occur. It was agreed, therefore, that the experiment should proceed with a design involving only control (= closed to fishing) and 'stock reduction' treatments. It was also considered preferable to impose the pulse fishing treatments in successive years in the interests of reducing the risks of results that depended on a single year of (possibly 'unusual') events, even though that strategy would be likely to increase the variance among 'replicate' reefs in the experimental treatment(s) without allowing examination of 'treatment x cluster x year' interactions. The preferred design options, therefore, were:

- i. Six clusters of four reefs, with two reefs per cluster closed to fishing (historically and in the future) and two reefs per cluster subjected to intensive fishing and then closure (for 5 years); or
- ii. Four clusters of six reefs, with two reefs per cluster closed to fishing (historically and in the future), two previously open reefs per cluster subjected to intensive fishing and then closed for 5 years, and two historically closed reefs per cluster subjected to intensive fishing for one year and then re-closed.

Intensive fishing treatments should be applied to one reef in each cluster in consecutive years. Each of the above designs has different strengths and limitations. The first design has three main advantages. Firstly, it would involve sampling at more locations (clusters) over the geographic gradient being targeted. This would result in more information about non-linearities in the response of fish stocks and/or the fishery to our manipulations than would be obtained in the second design. Secondly, the first design does not involve the relaxation of any existing

area closures to fishing. The design is theoretically more conservative, therefore, with respect to the conservation management strategies of the GBRMPA. Thirdly, it provides greater flexibility and power for future (potential) development of experimental trawl treatments to consider interactions between the effects of inter-reefal trawling and reef line fishing.

The second design has different strengths. First, the inclusion of a treatment involving fishing on historically closed reefs will provide considerably better information about the status and structure of relatively un-fished local stocks, and about the dynamics of the stocks and the fishery during initial fishing of such stocks. Inferences about local stock size from 'depletion estimates' (Hilborn & Walters 1992) will be considerably stronger for these reefs than for reefs on which stocks are already exploited. Second, the fishing of historically closed reefs will provide valuable insights for interpretation of comparisons of stock structure and catch rates between closed and open reefs. Without the information provided by the third treatment in this design, we have no direct estimates of the degree to which differences between closed and open reefs might reflect the effects of past fishing, and how much fishing is required to alter substantially the structure of reef-associated populations. Third, a key element of the experiment is testing empirically the relationship between harvest, catch rates, and fishery independent estimates of stock density. The value of this test relies heavily on the amount of change in stock density that can be imposed, and the range of densities over which the relationship between catch rate and fishery independent methods can be mapped. Clearly, fishing closed reefs will provide the maximum potential to impose marked changes in stock density and is the only mechanism of mapping the catch rate-independent method relationship at stock densities above those on already exploited reefs. Fourth, controlled stock reductions on relatively unfished reefs provides for more direct assessment of the 'recovery' of reefs after protection (through reef closure) from the effects of fishing. In the absence of this treatment, assessments of 'recovery' depend on the assumption that reefs that have been fished historically, and for which we have no 'starting condition' information, would have been generally similar to control reefs (that have been closed to fishing for some time) had they not been fished. Thus, recovery is measured exclusively as the degree to which fish populations on reefs that are at some point closed to fishing subsequently approach populations on control reefs. As the degree of similarity among reefs in population dynamics of target species decreases, this measure of recovery will become weaker. Where information exists about the status of reefs prior to the effects of fishing, fewer assumptions about the 'original' or unfished status of populations underlie measures of population recovery: recovery on a given

reef is measured against the starting conditions on that reef, as well as in the context of other control reefs. Such a design is likely to be more robust to substantial variation among reefs in such features as 'carrying capacity' and exposure to larval recruitment. Fifth, the three-treatment design provides direct tests of the potential utility of rotational or periodic closures of the fishery (or areas available to it) as a fishery management strategy. The use of area closures for fishery management is gaining increasing support, but largely has not been tested. There is some evidence from the Great Barrier Reef, for example, that although initial fishing pressure on 'virgin' grounds opened to fishing is substantial, catch rates decline rapidly to the point where those grounds appear no more attractive than surrounding grounds that have always been accessible, even though the stocks of fish on the recently opened grounds remain higher than in surrounding areas (Beinssen 1989a,b, Davies unpub. data). The second experimental design allows the direct and immediate test of the consequences of rotating closure and access to a fishery. It is also the only way in which to test directly the 'secondary' effects of fishing on non-target species (possibly through trophic interactions), because such effects, if real, almost certainly exist already on reefs that have been subject to a long history of fishing. Finally, the unilateral closure of reefs in the fishery without compensatory opening of reefs, albeit temporarily, is likely to reduce substantially the potential for endorsement of the work by the fishery. This is an important consideration, because the success of the experiment will hinge on the willingness of the recreational and commercial fishing sectors to a) comply with periodic closures, and b) provide researchers with detailed catch and effort information for the experimental and surrounding reefs.

The amount and immediacy of information to be gained from the second design far exceeds that obtainable (at least in the short-medium term) from the first. The main controversy with the second design is the fact that it involves relaxing closures to fishing on some reefs at least temporarily. There is clear need for a balance here between the desire to maximise the information gained from the expense of such a large-scale manipulation, and the environmental 'cost' of allowing fishing on reefs that have been protected from fishing for some years. We consider the trade-off to favour the second experimental design for three reasons. Firstly, the number of closed reefs to be opened to fishing is small (1.63% of all closed reefs in the GBRMP) and they will be opened to fishing for only one year. The environmental cost (to the GBR) and loss of virgin spawning stock from the GBR is thus almost certainly unmeasurably small. The potential to gain unique information for the future management of the fishery, however, is great. Secondly, the absence of sound historical information about the dynamics

of target fish stocks on reefs that have been subjected to many years of fishing weakens substantially inferences drawn from study of them, either under increased fishing pressure or during recovery after protection from fishing. Inferences about the effects of fishing and the dynamics of both stocks and fishery under changing conditions of fishing pressure will be strengthened considerably by the inclusion of the third treatment - ie., allowing fishing on a small suite of protected reefs. Finally, the importance of cooperation from the fishing fleets cannot be overstated. Adequate information about the effort and catch of both commercial and recreational fishing fleets, especially on the experimental reefs, is critical. The scale of the GBR and the proposed experiment make the acquisition of detailed catch and effort information through surveillance impossible. The information can only be obtained with the cooperation of the fleets, and verified with affordable levels of enforcement and independent surveillance. Further, the cooperation of the fishing fleets in imposing the additional effort is essential. Again, this is a logistic and cost consideration. Given information we now have about the magnitudes of catches routinely taken from reefs in the GBR, it would be unaffordable to 'swamp' that effort with purchased research fishing effort. The only alternative is a combination of effort supplied by the existing fleets and carefully structured catch surveys. Extensive consultation with all sectors of the fishery indicate that such cooperation is far more likely with the second design than with the first.

Implementation of Experiments

Imposing Fishing Treatments

We have had considerable discussion with researchers and fishers about the mechanisms available for imposing the pulse-fishing effects on experimental reefs. In particular, there was concern about the potential to impose substantial reductions of reef-associated stocks. Discussion of the issue has been hampered by the absence of any estimates of the absolute per-reef stock size on the GBR, except that for a single reef provided by Beinssen (1989a). Catch rates were well documented for professional fishing crews by Davies (1993, 1994), albeit under constraints on fishing practice imposed to fulfil research objectives, and for recreational fishing by club anglers by Russ (in prep) and Higgs (1993). Typical catch rates for professional fishers were available from private records discussed with Davies & Mapstone by some professional fishers. These figures suggested that a team of 4 professional fishers, operating under some constraints of fishing practice, could be expected to take at least 150 coral trout per day, and up to 250 per day when fishing 'at will'.

Given these figures, and a notional budget of \$150,000 annually for stock reductions on 4 reefs in each year, it was expected that, allowing for some decline in catch rate with the progress of fishing, between 2,000 and 3,000 coral trout could be taken off each treatment reef in the year of pulse fishing. Professional fishermen have reported that catch rates often decline after one or two days fishing on a reef (anecdote, private logbooks), and so the above figures were estimated on the assumption that fishing would be by intermittent visits of about 2 days to each reef. Beinssen (1989) observed about a 25% reduction in estimated stock size over 14 days of continuous fishing, despite a substantial drop in catch rate. We considered that a greater reduction than observed by Beinssen would be required to impose a fishing mortality of at least twice ambient levels on the experimental reefs, and impose sufficient stock reduction for the experiment to be considered secure. Given that the modelling concentrated on experimental scenarios in which experimental fishing imposed a 3-fold increase in fishing mortality during the years of manipulations, it is considered imperative that the budget for the imposition of the experimental treatments be increased to the maximum possible, whilst still being able to afford annual monitoring of the reefs. Recent information from the commercial fishery indicates that annual catches from individual reefs can regularly exceed 5000 individuals. Under these conditions, it is unlikely that we would be able to impose sufficient additional fishing effort by charter to achieve the desired three-fold increase in catch. Further, concerns were raised by fishers that effort imposed without careful consideration of usual fishing practice would jeopardise the relevance of the research to the expected growth of line fishing on the GBR, and the acceptance of results by the fishery.

We recommend, therefore, that additional effort be imposed on experimental reefs through a combination of structured research catch surveys using fishers under contract, and additional effort applied by the existing fishing fleets. The mechanisms for increasing ambient effort should be through more frequent fishing of selected reefs than occurs now, but usual fishing practice should not be changed otherwise. Limited experience so far with the commercial fishing fleet indicates that under these circumstances reliable catch and effort information will be provided to researchers by fishers, provided their identity remains confidential.

It is desirable to impose the additional fishing pressure by as many fishing methods as possible, with special emphasis on those employed by recreational and commercial fishers routinely. Involvement of skilled recreational and professional fishers in the manipulative stages will enhance liaison between researchers, management, and users, and provide valuable information about the

reactions of fishers to declining stocks, assuming that catch rates also decline over the period of the manipulations. In addition to the mainstay contracted fishing effort, several alternatives for enhancing effort have been discussed. Five main methods are recommended:

- i. Requests for additional cooperative effort by local or passing commercial fishermen.
- ii. Requests for fishing charter vessels to routinely fish the experimental reefs in the year(s) of manipulation.
- iii. Encouragement of recreational angling clubs to fish target reefs, accompanied by at least one research officer.
- iv. Sponsorship of recreational fishing competitions to stimulate involvement of the small boat recreational fleet and obtain data about their fishing characteristics.
- v. Sponsored 'invitation only' prestige spearfishing competitions.

In each case, additional relevant data should be sought either by attendance of technical staff or through voluntary log-books kept by fishing vessel skippers.

For maximum catch under controlled and monitored conditions, a consistent team of highly skilled commercial fishermen should be used for catch surveys throughout the study. Saleable catch should be sold by the commercial team to cover their costs and normal expected income, with profit sharing between the research project and the commercial team to be negotiated in order to offset the costs of vessel charter. Resultant savings over anticipated costs of systematic fishing should be used to buy additional fishing effort to maximise the magnitude of stock reductions on reefs, provided that stocks are not reduced beyond the levels necessary to obtain robust 'depletion' estimates of local stock size and verify the relationship between catch rates and stock densities.

Consistency of fishing crew is essential to allow legitimate comparisons of fishing characteristics (CPUE, catch) among reefs, clusters, and years. Active commercial fishermen should be contracted and fishing should reflect usual fishing practice so that the results are directly translatable to industry. At least some fishing would have to be more structured than usual practice, however, in order to provide systematic data for spatial and temporal comparisons of fishing characteristics and stock structure. We recommend, therefore, that each reef be visited for 2 days at a time, with one day being structured fishing

and the other being 'at will' fishing. Skilled technical staff should go on every fishing trip to process samples and record data about the fishing activities and success.

Critical Data

Several types of data should be collected from the experimental reefs:

- ?? Fishery independent estimates of abundances of target and non-target species;
- ?? Fishery dependent measures of abundances of target species;
- ?? Age- and size-structure information for the target species;
- ?? Fishing behaviour by recreational and commercial fishers;
- ?? Estimates of ambient (and illegal) fishing effort during the experiment;
- ?? Reproductive status of target species before and after stock manipulations, if feasible.

We discuss the main considerations for these below. Note that it was concluded at the workshop in July 1994 that measuring inter-reef movement of target species should not be a high priority for the ELF Experiment because: i) Davies' work indicated convincingly that coral trout were highly sedentary and Beinssen's work (1989b) indicated the same for *Lethrinus miniatus*, perhaps the second priority target species over much of the GBR; and ii) tagging work would be very expensive and time-consuming, and, given recent work, not sufficiently important to displace collection of the above types of data.

Fishery-independent Estimates of Abundance

The only feasible strictly fishery independent method of assessing the abundances of targeted species and their prey was considered to be visual surveys of fishes by divers on SCUBA. The methods for such surveys are well established (Fowler 1987, Mapstone & Ayling 1993, Sale & Sharp 1983, Samoily & Carlos 1992), though restricted in application to shallow water (<10m depth) by diving regulations. It was agreed (July 1994) that visual survey should, therefore, be the primary method for monitoring the direct and secondary numerical effects of fishing on shallow reefs. All reefs should be sampled twice annually, with one of the samples being between April and June each year to ensure that young-of-the-year coral trout, which settle in November-January (Doherty unpub. data), could a) be counted easily (*i.e.* were non cryptic) and b) separated reliably by size from older individuals (Ayling & Ayling 1993, 1994). The second survey would provide increased precision in annual estimates of abundances, some measure of intra-annual variation in that estimate, and a safe-guard against failure to

obtain data from some or all reefs in the other survey or unusual events that coincided with the Autumn survey. Apart from the results of our modelling, in which sub-sampling intensity was found to be important when nuisance variation was large, we considered this important because each reef was expected to be surveyed in a single day, and the costs of vessel time precluded lengthy delays in the survey schedule to accommodate, for example, bad weather. Most researchers favoured timing the second survey each year to immediately precede the spawning season, and thus provide an index of spawning stock abundances. It was agreed that surveys should encompass the reef perimeter. With a maximum of 30 transects feasible within a single day, the reefs would be sub-sampled by six-ten sites of five-three transects, the details to be resolved with development of the detailed proposals for other aspects of the work. All sites should be identified by GPS records, and visual surveys should be conducted consistent with existing best practice (Ayling & Ayling 1993, 1994, Halford & Thompson 1994, Mapstone & Ayling, 1993).

We recommend also additional visual surveys during the controlled fishing years, at least on the reef being fished that year and one control reef in each cluster. These surveys, which should be matched closely with the spatial distribution of structured fishing, will be important for three reasons: firstly, to provide fishery independent measures of the status of target stocks in shallow water with which to compare changes in CPUE; secondly, to provide an independent series of 'catch rate' vs cumulative 'catch' data from which to estimate original (pre-reduction) stock size; and thirdly, to test the utility of underwater visual surveys for routine stock assessment during periods of expected change in stock density. The test assumes that stock density changes as a result of intense fishing, and that harvest rates are not compensated by immigration of fish during the year. Some assessment of whether the latter occurs will be possible by analysis of the progressive age-specific harvest rates in the context of initial age-structure information.

Fishery-dependent estimates of Abundance & Fishing Behaviour

Careful records of catch (by species and size) and fishing effort for all types of fishing must be kept throughout the work. For initial (1995) and final (1999) sampling of all reefs to provide age-structure data (below), CPUE data will provide valuable insights into regional effects of reef closure on catch rates. Data should be recorded by dory, 'session' (morning/afternoon), and site on each reef. An observer should accompany all dory-men at some times in order to collect additional data to those being recorded by the fisher, and to verify the fisher's data.

Fishers should be interviewed formally (but briefly) at the end of each day to assess their responses to fishing on each reef.

During the experimental fishing (1996, 1997, 1998, 1999), similar catch and effort data must be recorded, both during structured fishing and 'at will' fishing. It is important also during these periods that catch and effort data be recorded from all sources of fishing on the experimental reefs. Catch and effort data should be geographically and temporally related closely to the distribution of visual survey data. Interviews with fishers should be done at several times during the manipulations to gauge their responses to the effects of intensive fishing on their usual fishing practice. Catch rates by age should be calculated at several times during the experiment in order to assess the likelihood that substantial age-specific immigration onto experimental reefs might compensate for local stock reductions.

Limited, controlled fishing on experimental reefs should continue following closure of reefs that were subject to stock reduction. The objective of fishing during post-closure years should be to provide CPUE data for reefs during their recovery phase, without seriously reducing target stocks. Hence, relatively few fishing trips should be made (4 per year), with each trip restricted to one day. Fishing visits to each reef should correspond with visual surveys of each reef in each year, so that results for CPUE from line fishing during the 'recovery' phase can be compared with visual survey results. As far as possible the regular team of commercial fishers should do the fishing, catch should be sold, and costs to the project should be minimised (possibly to zero) through profit-sharing and/or industry cooperation.

Size- and Age-structure Data

It was at first intended that age-structure data be obtained from each reef in each year. This proposal has been reduced to include only the following age-structure sampling:

1. All reefs in only the first and final years of the proposed experiment;
2. At several stages during the experiment, but only from the manipulation reefs and selected 'unfished' reefs;
3. As opportunity arose at other times (e.g. during monitoring of fishing characteristics following closure of experimental reefs).

The above (reduced) sample set was recommended, firstly, because of concerns about the potential to process the large numbers of otoliths collected annually. Assuming a minimum sample size of 200 coral trout per reef per year (given expected longevity of 15 years), 4,800 otoliths would need to be processed each year for *Plectropomus leopardus* alone. Secondly, there was concern generally about the potential for annual samples from control reefs to modify the stock structure on those reefs, thus reducing their 'control' value. Thirdly, because coral trout (and all secondary targeted species) live considerably longer than the expected duration of the experiment, annual age-structure data were expected to offer little important information over samples separated by up to 5 years. Fourthly, the loss of other (more) valuable information that would not be collected if limited staff time was fully consumed with aging annual samples was considered an unacceptable cost of annual samples. In particular, we consider information about the rates of extraction of different aged fish during periods of increased fishing pressure of greater interest than simple age structure information from all reefs, and so considerable effort should be directed to measuring those age-specific catch rates. If time was available it should be devoted to additional samples for coral trout, or assessment of secondary species. Budget considerations were also important, it being necessary to reduce either the visual survey work or the age-structure work in order to maximise the budget for stock reduction effort in each year. The visual survey work was considered particularly important to maintain since it provides the only fishery independent data about abundances of target species and their prey.

Concern has been expressed over potential bias in age-structure information derived from line-caught samples because of age or size specific variations in catchability and gear selectivity. Accordingly, it has been suggested that samples be collected from each reef by spearing on SCUBA. In spearing over a designated area, every effort should be made to spear every fish (of the main target species) seen and strict rules of target selection must be devised for instances when more than one target individual is visible at the same time. The assumption in this recommendation is that the added control over target selection afforded by spearing should minimise age or size specific biases in age-structure information, at least for coral trout more than about 6 months old (~20cm total length).

Background Fishing Effort

Surveillance of experimental reefs and estimates of (illegal) effort will be critical for the interpretation of the experimental results. As discussed earlier, there is considerable anecdotal

evidence that infringements of fishing closures on the GBR are common, but past surveillance has proved ineffective in either deterring infringement or providing estimates of the degree of infringement. In this context, it might actually be misleading to alter rates of infringement at all since any changes in stock density and/or catchability on control (putatively closed) reefs during the experiment will make interpretation of the contrasts between those reefs and treatment reefs difficult. Whilst the importance of better surveillance data on experimental reefs has been emphasised at several workshops about the experiment, it was also acknowledged that ready mechanisms for either regular surveillance or enforcement of closures were lacking. A dedicated surveillance programme would be prohibitively expensive. In the absence of effective enforcement of closures, it may be more sensible to leave the *status quo* alone and assume no change in illegal fishing behaviour than to have to attempt to 'guess' the way in which illegal behaviour has changed. Under these conditions, however, estimates of the rates of infringement will be vital for inferences of the effects of different fishing regimes. Three approaches to the problem have been suggested: i) redirect existing aerial surveillance to increase frequency and reliability of observations on experimental reefs; ii) seek the cooperation of industry in observing at least those closures associated with the experiment, and to foster an element of 'self policing'; and iii) increase the frequency of visits to experimental clusters by Boating & Fisheries patrol vessels and/or Department of Environment and Heritage vessels. It was stressed that as far as possible the emphasis should be on cooperation and surveillance rather than enforcement.

Reproductive Biology

Whilst there are clear reproductive biological implications of fishing a protogynous hermaphrodite species like *P. leopardus*, detailed studies of reproductive biology were considered of lower priority than other components of the work. Since the budget was already stretched, it was considered undesirable to replace measures of fishery relevant data (from line fishing) or independent estimates of stock size (from visual surveys) with studies of reproductive biology. We recommend, however, that at least gross reproductive staging of individuals be done wherever possible, and that gonads be preserved for use by external projects, if such projects arise. Such samples would be particularly informative if taken at the beginning of the stock reduction work and during the reproductive season in the year following stock reduction to assess whether increased fishing has affected grossly the age and/or size at reproduction and/or sex change.

Logistic Considerations & Coordination

We envisage the ELF Experiment being done as a set of closely related but free-standing research tasks, each led by senior staff from the partner institutions in the CRC. The tasks and notional budgets and responsibilities for them are given in Table 11. Orchestration of the logistics, economics, and design of such manipulations will constitute key responsibilities to ensure the success of the experiment. Detailed planning of the fieldwork components to ensure coherence of data from different tasks will be coordinated by the project leader and post-doctoral fellow in the Effects of Fishing Project. Quarterly meetings of research and technical staff across the whole project will be convened to discuss progress, difficulties, potential publications, and amendments to the programme. An annual workshop to synthesise the data from each task and review the project in the light of data collected to date will be mandatory for all participating researchers. Annual reports on all research are required by the CRC, and for this project we recommend external review of those reports, at least in the first two years of the experimental manipulations. Invitation of relevant researchers from outside the project to the annual workshops should also be considered, especially following the first two attempted stock reductions.

It is critical that agreements pertaining to processing of and access to data, intellectual property, publication, reporting, and dispute resolution be explicitly negotiated before the project fieldwork begins. The potential for disputes over intellectual property, publication, data access and unforeseen matters in such a venture is greater than usual. Whilst we will attempt to avoid such conflicts by discussions at the quarterly and annual meetings, we will also formally convene meetings of senior non-involved staff to resolve otherwise intractable disputes. The composition of the meetings will vary depending on the parties involved in each dispute, but will generally involve a core of: the director of the CRC, the leader of Programme 2, and the project leader(s) for Project 2.4. In addition, a senior representative from each institution whose staff are involved in the dispute will be invited to attend, and involved parties interviewed. The progress and proper conduct of the research would benefit also from convening of a 'steering committee' comprised of senior representatives of participating government organisations, especially management agencies, and peak fishing representatives.

Table 11: Major task areas within the proposed CRC ELF Experiment, indicating principal researchers, institutional affiliations, and notional 'bottom line' annual budgets. A ? indicates that either the work depends on earlier results (for spearfishing) or the status of the task and/or the investigators role in the ELF project are uncertain at this stage (for Reproduction). Nil budget tasks are either supported externally (Economics), or may be accounted for in other major task budgets (Fisher responses, spearfishing).

Task	Leaders	Institution	~Budget (\$000)	Years
Visual Survey	Williams/Ayling	AIMS	150 (+20)	All (96-9)
Age-structure				
- line	Russ/Brown	JCU/QDPI	83	All
- spear	Davies/Mapstone	JCU/AIMS	Nil	95, 99 (?)
Manipulations	Mapstone/Davies	JCU	198, 150	95-9
Catch-Effort	Davies/Mapstone	JCU	5	All
Fisher response	Davies/Robertson (?)	GBRMPA	nil	All
Modelling	Smith/Campbell	CSIRO	15 ^z	All
Economics	Robertson	GBRMPA	nil	95-8
Reproduction	Samoilys (?)	QDPI (?)	Nil	?
Coordination	Mapstone	JCU/CRC	5	All

^z Additional funds of ~ \$50,000 - \$100,000 per annum will be sought externally in 1998-2000.

CONCLUSIONS & RECOMMENDATIONS

The CRC for Sustainable Development of the GBR has provided an important institutional focus for the development of large scale experimental research into the effects of line fishing on the GBR. Implementation of the work we discuss here will significantly aid the examination of existing and future management options for maintenance of current fishing standards. Computer simulations of the population dynamics of the main target species, *Plectropomus leopardus*, based on recent field research, indicate that large scale experiments utilising whole coral reefs as units of experimental manipulation are feasible. Experiments can be designed such that the resulting field data will have good statistical power to detect effects of fishing, and measure responses of fished stocks to protection from further fishing. Such information is not currently available for the GBR reef line fishery, but will be critical to successful management of this recreational and commercial fishery.

We recommend an experimental design involving 4 clusters of 6 reefs spread between Cape Flattery in the north and the Swain Reefs in the south of the GBR. Three treatment regimes should be applied within each cluster.

- i. A *closed control* treatment should be represented by 2 reefs per cluster that have been closed to fishing historically and remain closed during the experiment, and which provide our best estimates of virgin stocks.
- ii. An *increased fishing* treatment, represented by two reefs per cluster that were historically open to fishing at will, which are fished with greatly increased intensity for one year, and are then closed to all but infrequent controlled fishing for 5 years. These provide our best estimates of the capacity of already fished stocks to withstand more fishing, and the dynamics of stock recovery after protection from fishing.
- iii. An *initial fishing* treatment, in which two reefs per cluster that have been closed to fishing for 5-12 years are opened to ‘at will’ fishing for one year and then re-closed. This treatment will provide our best estimates of the relationship between trends in catch rate and changes in stock density, the size(s) of unfished stocks, and the responses of fish stocks and fisheries to rotational harvest strategies.

Data to be collected from each reef in each cluster is indicated in Table 12.

The experimental work must be complemented with sound estimates of the distribution and intensity of both recreational and commercial line fishing over the GBR region. The main source of data about the commercial fisheries will be the compulsory log-book system managed by QFMA, but we recommend additional sampling of the commercial fleet as part of this experimental work. Such work will provide additional information about the reef-scale fishing and catch characteristics of the fleet and, managed carefully, greatly improve collaboration between the research project and the fishing industry. This component of the work will cost little, but is essential to the sensible and acceptable transfer of results from the experiment to management of the fishery.

Provision of adequate catch and effort information for the recreational fisheries is more difficult than for the commercial fleet. There have been some past attempts to estimate recreational fishing catch and effort information within one year (see Higgs 1993, Higgs *et al.* in prep for reviews), but there are no formal longitudinal research data available. Compilation of angling club records (with the cooperation of the clubs), the recent implementation of a log book system for fishing charter boat operators, the imposition of bag limits in 1993, and increased political focus on the recreational fisheries represent positive steps toward the provision of essential information about recreational fishing on the GBR. The CRC has initiated two projects to provide robust estimates of recreational reef line and spear fishing, and negotiations with relevant management agencies for the establishment of two long-term appointments to focus specifically on recreational fishing in the region has begun.

Computer modelling should be seen as an integral part of the project throughout. The emphasis of such work should be on investigating responses of and consequences for fisheries to different assumptions about population dynamics of target species and alternative potential management strategies. Furthermore, for a target species as sedentary as coral trout appear to be, the evaluation of management strategies such as area closures on the GBR as a whole will be dependent on our understanding of processes controlling larval dispersal. Accordingly, oceanographic and hydrodynamic modelling should be considered as tools for the extension of this project to GBR-wide recommendations.

Careful coordination among the research tasks within the experiment will be critical to the synthesis of the various data sets, and it is important that formal and informal procedures for the discussion of progress and dispute resolution be implemented from the outset. The project must be subject to peer review at regular intervals.

Table 12: Schedule of minimum data to be collected in each year from each reef in each cluster in the planned CRC ELF Experiment. \emptyset => data not collected; \emptyset => data collected; 'x i' => i multiple samples for each reef in that year; ?=> data may be collected, depending on either interest, funding, or the results of earlier work. FC=> 'fished & closed' (*increased fishing*) reef; OFC=> 'open, fished, & closed' (*initial fishing*) reef.

DATA	Reef	YEAR					
		1994-5	1995-6	1996-7	1997-8	1998-9	1999-00
Visual Survey	Control 1		\emptyset x 6	\emptyset x 2	\emptyset x 2	\emptyset x 6	\emptyset x 2
	Control 2		\emptyset x 2	\emptyset x 2	\emptyset x 6	\emptyset x 2	\emptyset x 2
	OFC ₁		\emptyset x 6	\emptyset x 2	\emptyset x 2	\emptyset x 2	\emptyset x 2
	OFC ₂		\emptyset x 2	\emptyset x 6	\emptyset x 6	\emptyset x 2	\emptyset x 2
	FC ₁		\emptyset x 2	\emptyset x 6	\emptyset x 2	\emptyset x 2	\emptyset x 2
	FC ₂		\emptyset x 2	\emptyset x 2	\emptyset x 2	\emptyset x 6	\emptyset x 2
Age Structure	Control 1	\emptyset	\emptyset	\emptyset	\emptyset	\emptyset	\emptyset
	Control 2	\emptyset	\emptyset	\emptyset	\emptyset	\emptyset	\emptyset
	OFC ₁	\emptyset	\emptyset x 4	\emptyset	\emptyset	\emptyset	\emptyset
	OFC ₂	\emptyset	\emptyset	\emptyset	\emptyset x 4	\emptyset	\emptyset
	FC ₁	\emptyset	\emptyset	\emptyset x 4	\emptyset	\emptyset	\emptyset
	FC ₂	\emptyset	\emptyset	\emptyset	\emptyset	\emptyset x 4	\emptyset
Catch & Effort	Control 1	\emptyset	\emptyset x 6	\emptyset	\emptyset	\emptyset x 6	\emptyset
	Control 2	\emptyset	\emptyset	\emptyset	\emptyset x 6	\emptyset	\emptyset
	OFC ₁	\emptyset	\emptyset x 6	\emptyset	\emptyset	\emptyset	\emptyset
	OFC ₂	\emptyset	\emptyset	\emptyset x 6	\emptyset x 6	\emptyset	\emptyset
	FC ₁		\emptyset	\emptyset x 6	\emptyset	\emptyset	\emptyset
	FC ₂		\emptyset	\emptyset	\emptyset	\emptyset x 6	\emptyset
Surveillance	All	\emptyset	\emptyset	\emptyset	\emptyset	\emptyset	\emptyset
Fisher Response	All	\emptyset	\emptyset	\emptyset	\emptyset	\emptyset	\emptyset
Reproduction	All (?)	\emptyset	?	?	?	?	?

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APPENDIX 1: Modelling Population Dynamics

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We here describe in detail the main features of the population dynamics models central to the REEF programme, as we implemented it. We discuss how stochastic variation is introduced into the output data, the way in which (some) user inputs affect model parameters, and discuss various assumptions underpinning our use of the models. We assume that the body of the document *Design of Experimental Investigations of the Effects of Line and Spear Fishing on the Great Barrier Reef* has been read prior to reading this appendix.

Larval Supply & Recruitment

Much of the stochastic variation in our population dynamics models was introduced *via* models of the supply of larvae to reefs and the transition from larval stage, through settlement to an age of 1 year post settlement (which we defined as recruitment). Although we also allowed for variation in post-recruitment processes, especially mortality, the most likely geneses of great variations in populations of reef fish are the dispersive larval phase and the settlement and early juvenile stages.

Larval Dispersal and Links Among Reefs

The original REEF program simulated larval dispersal over the whole GBR in order to provide rough assessments of links among reefs and estimates of larval input onto candidate reefs for experimental manipulation. The routine was not intended to provide a “correct’ or optimal” description of larval dispersal over the whole GBR but a simple framework for modelling ‘realistic scale effects ([such as] distances of larval dispersal, linkages, etc.)’ (Walters & Sainsbury, 1990). Although we retained this routine in the revised programme, it was not used to generate the background larval loading to each experimental reef. There were two reasons for this change: 1) the simplicity of the dispersal routine left it open to challenge as being unrealistic (even though that was not its principal purpose), and possibly misleading; and 2) by setting the larval supply on each reef directly, we had greater control over the characteristics of variation in recruitment - *i.e.* entry to the reef associated system.

?

Larval Supply to Reefs

In Walters' & Sainsbury's (1990) original simulations, larval supply (**L**) to each experimental reef (*i*), was assumed to consist of four components: ?

- i. **SL_i**, the total Larval production Spawned on reef *i*;
- ii. **BL_i**, the Background Larval supply to reef *i* from all other (non-experimental) reefs, calculated from an average (assumed) per-reef larval production on all reefs and linked to reef *i* by the dispersal model;
- iii. **EL_i**, the sum of Larvae supplied to reef *i*, *via* the dispersal model, from other Experimental reefs; and
- iv. **PL_i**, additional stochastic 'Pulses' of Larvae arising from unknown sources.

The gross index of larval supply to reef *i* was given by:

$$\mathbf{L}_i = ss*\mathbf{SL}_i + (1-ss)*[\mathbf{BL}_i + \mathbf{EL}_i] + \mathbf{PL}_i \quad (\mathbf{A0})$$

Where *ss* was the 'self seeding' coefficient, expressed as the proportion of larvae spawned on reef *i* that subsequently settled on that reef, and was assumed to be constant among all reefs.

The value of *ss*, which was set by the user, would be expected to diminish rapidly with increasing length of (planktonic) 'larval' (pre-settlement) life beyond that interval within which particles would be expected to be retained in the vicinity of a reef by hydrodynamic features such as tidal eddies (? 5 days, K. Black pers comm.). Since the dispersal model takes no account of such potential for larval entrapment by (*e.g.*) tidal eddies, the degree to which nearby (experimental) reefs would contribute to the supply of larvae to reef *i* (**EL_i**) would also vary inversely with the length of larval life set in the model code. Walters & Sainsbury (1990), in the absence of evidence to the contrary, set a relatively short larval life for coral trout (4 days), and so self-seeding and seeding from adjacent reefs was relatively influential in the determination of **L_i**. P.J. Doherty & A.J. Fowler (AIMS) have since verified that the planktonic life of coral trout is about 27-31 days, and we set larval duration to 30 days accordingly. This resulted in vanishingly small values for **EL_i**. We set *ss* at the arbitrary value of 0.05.

The larval production from each reef (**SL**) or group of reefs (**BL**, **EL**) was calculated from the index of adult spawning abundance using Beverton-Holt recruitment equations of the form:

$$\mathbf{SL}_i = f * \mathbf{A}_i / (1 + f * \mathbf{A}_i / k)$$

where:

\mathbf{SL}_i = net number of Larvae produced on reef i and surviving to settlement;

f = (mean adult fecundity) * (maximum rate of larval survival to settlement in the absence of density dependent mortality of larvae);

\mathbf{A}_i = number of Adult females spawning on subject reef i , or the average other experimental or non-experimental reef; and

k = larval ‘carrying capacity’, possibly reflecting density dependence of larval survival prior to settlement.

When k is large, larval settlement is effectively proportional to adult abundance over the whole GBR - *i.e.* recruitment to reefs is not limited by processes during the larval stage. When k is small, larval supply is effectively independent of adult abundance except when total egg production is very low - *i.e.* recruitment would be limited mainly by larval-stage processes.

In the original model, larval carrying capacity (k) for individual reefs (\mathbf{SL}_i & \mathbf{EL}_i) was scaled over a two-fold range from the north to the south of the GBR. This scaling was presumably included on the assumption that the observed north-south increase in abundances of coral trout (Ayling & Ayling, 1986, 1992) would be at least partially reflected in differential local contributions to larval abundances when self-seeding or recruitment from nearby reefs was important. The carrying capacity applied to the calculation of background larval supply (from all reefs) was the average of the (scaled) values for individual reefs, and so was the same over the entire GBR. Hence, when local- or self-seeding was trivial, no north-south gradient in larval carrying capacity would be effective. This was the default situation in our modelling, since we assumed a larval (=pre-settlement) life of about 30 days, with only slight (0.05) potential for local self seeding.

This may be inappropriate, however, since with increasing length of larval life, and decreasing potential for local larval retention, the influence of hydrodynamic dispersal on the distribution of

larvae among reefs should increase. Hydrodynamic studies have indicated that the southerly flow of GBR waters is negligible to the north, but increases in strength south of about Cairns. Hence, the relative contributions of local *and* global supply of larvae might be expected to vary north-south. Further, background larval supply might be expected to be greater further south because those reefs received the accumulated contributions of larvae from a vast number of reefs to their north. Any clines in larval carrying capacity should perhaps be expressed, therefore, in default calculations of both local and background larval supply.

In our implementation of the REEF programme, however, the default level of background larval loading (**BL**) was assumed to be constant for all reefs and not dependent on the dispersal model. We then set a (user definable) ‘scaling factor’ which scaled the base value of **BL** so that there was a linear n -fold variation in background larval supply across clusters. When $n=1$, \mathbf{BL}_i was the same for all clusters, and when $n>1$, \mathbf{BL}_i differed linearly among clusters. For example, for 2 clusters with a 3-fold scaling, the background larval loadings for all reefs in a cluster would be $\mathbf{BL}/2$ and $3\mathbf{BL}/2$ for clusters 1 and 2 respectively. This control allowed us to model explicitly potential geographic differences between clusters, rather than attempt to generate such effects by varying the simple dispersal model.

The (unscaled) value for **BL** was calculated from the mean abundance of reproductive adults on all nominated experimental reefs, and this average was accepted as representative of the GBR-wide average per reef abundance of adults. This approach encapsulates two assumptions: i) that the proportion of experimental reefs open to fishing and closed to fishing prior to the imposition of additional fishing pressure satisfactorily mimics the proportion of reefs subject to little fishing or moderate fishing reef wide; and ii) that following the imposition of increased fishing on treatment reefs, the abundances of adults on experimentally fished reefs is either a) a useful surrogate for abundances reef-wide under a (future scenario) of increased fishing over the entire GBR, or b) an approximate compensation for the over-representation of closed reefs in the experimental set relative to the global fraction of closed reefs.

Assumption i) is almost certainly false. Approximately 5% of the reefs on the GBR are notionally closed to fishing, whereas 33-50% of the experimental reefs are closed to fishing.

Further, in most cases, we assumed closure to fishing to be completely effective, whereas this is almost certainly not so for at least some of the closed reefs in the GBR. On the other hand, however, fishing pressure is likely to vary over the GBR, with some reefs open to fishing suffering little fishing pressure.

Assumption ii) may be legitimate in the year of manipulation or the following year, but is likely to become increasingly in error for both options a) & b) as populations on experimental reefs recover toward virgin biomass following protection from fishing. Indeed, as the populations on treatment reefs approach those on control reefs, the generation of values for \mathbf{BL}_i will approach those expected of a system free of fishing.

The importance of these assumptions on the simulation results will be manifest most strongly under population regulation hypothesis H_3 & H_4 (see main text) since it is in these scenarios that larval supply is strongly dependent on adult densities. The importance of the assumptions would be negligible for H_1 & H_2 . Errors in either or both assumptions are most likely to result in higher estimates of average adult stock size than in reality and, therefore, higher rates of background larval supply. Hence, the recovery of fished stocks in our simulations might be more rapid than would occur in the field. This was not of great concern to us, because more rapid recovery would mean that assessments of the power to discriminate treatment-control contrasts would diminish with increasing distance (in time) from the year of stock manipulation more rapidly than if the assumptions were correct in all years. Hence, we would get a more pessimistic assessment of the potential experimental designs.

We also chose a different mechanism from Walters & Sainsbury (1990) for generating stochastic variation in larval supply (see below), and dispensed with the parameter PL_i . Thus, the deterministic part of (A0) effectively was simplified to:

$$\mathbf{L}_{ij} = ss * \mathbf{SL}_{ij} + (1-ss) * c_{.j} * \mathbf{BL}_{.j} \quad (\mathbf{A1})$$

where:

\mathbf{L}_{ij} = Larval supply to reef i in cluster j ;

ss = the self-seeding coefficient;

\mathbf{SL}_{ij} = number of Larvae produced on reef i in cluster j and surviving to settlement;

$c_{.j}$ = the scaling factor for cluster j ; and

$\mathbf{BL}_{..}$ = the overall mean **B**ackground supply of **L**arvae from all other reefs.

For p clusters to be scaled over an n -fold range, the scaling factor for the j th cluster is:

$$c_j = 2[p-1+(j-1)(n-1)]/[(p-1)(n+1)] \quad (i=1\dots p).$$

Stochastic Variation in Larval Supply

The value of \mathbf{L}_{ij} generated from (A1) was taken as a ‘long-run’ mean level of larval supply for each reef i , in cluster j . We then allowed for stochastic inter-annual variation about that mean, generated by three effects:

- i. **VG**, the **Global mean inter-annual Variation**, common to all reefs in all clusters;
- ii. **VC**, a **Cluster-specific component of inter-annual Variation**; and
- iii. **VR**, a **Reef-specific component of inter-annual Variation**.

Explicitly, stochastic variation for reef i in cluster j was modelled as a log-normally distributed effect, resulting in:

$$\mathbf{L}_{ij} = [ss\mathbf{S}\mathbf{L}_{ij} + (1-ss)c.j\mathbf{B}\mathbf{L}_{..}] * e^{\mathbf{VR}_{ij} + \mathbf{VC}_j} \quad (\text{A2})$$

where:

$$\mathbf{VR}_{ij} = z_1 * (\mathbf{VG} + z_2 * ?_{\mathbf{VGR}}),$$

$$\mathbf{VC}_j = z_3 * ?_{\mathbf{VGC}},$$

and:

$z_n, n = 1,2,3$ are random normal deviates,

$?_{\mathbf{VGR}}$ = standard deviation among reefs (within clusters) in **VG**,

$?_{\mathbf{VGC}}$ = standard deviation among clusters in **VG**.

The three parameters **VG**, $?_{\mathbf{VGC}}$, and $?_{\mathbf{VGR}}$ can be varied by the user. Further, the variation introduced here can be set to be independent for each cluster and/or reef within a cluster or similar for all the clusters and/or reefs in each year. For example, if the normal deviates z_n ($n=1, 2, 3$) are independent in each year, then each reef and cluster behaves independently. If z_3 is set the same for each cluster in a given year, then the cluster-scale variation from the deterministic value of \mathbf{L}_{ij} is the same for all clusters in that year - *i.e.* clusters act coherently. Similarly, all reefs can be made to act somewhat coherently within a year by setting z_2 to be the same for all reefs in that year. If both z_2 and z_3 are the same in all years, then larval supply is largely synchronous at both reef and cluster scales - *i.e.* a given year is either ‘good’,

‘bad’, or ‘mediocre’ for all reefs. Some variation among reefs is retained in all years, however, by setting z_l independently for each reef in each year.

Recruitment to reefs

Larval supply to each reef, L_{ij} , is next translated to abundance of juveniles at age 1 through a second Beverton-Holt (recruitment) relationship:

$$\mathbf{J}_{ij,1} = s_0 * \mathbf{L}_{ij} / [1 + (s_0 * \mathbf{L}_{ij} + \mathbf{JT}_{ij} + \mathbf{A}_{ij})/k'] \quad (\text{A3})$$

where:

$\mathbf{J}_{ij,1}$ = the number of **J**uveniles reaching age 1 on reef i in cluster j ;

s_0 = the (overall) average rate of survival from settlement to age 1;

\mathbf{JT}_{ij} = the **T**otal number of **J**uveniles on each reef prior to addition of the new cohort;

\mathbf{A}_{ij} = the number of **A**dults on each reef; and

k' = juvenile ‘carrying capacity’.

Setting k' large results in a ‘recruitment-limited’ population in which the relative abundances of cohorts are proportional to their relative abundances at larval settlement. Setting k' small results in populations in which abundances are limited by post-settlement density dependent processes which increase in importance as recruitment increases. We used a (arbitrary) value of 0.4 for s_0 in our simulations, but a component of inter-annual variation in that rate was allowed (see below).

There was assumed to be a two-fold increase in juvenile carrying capacity (k') north-south from Cape Flattery to the Capricorn-Bunker Group, producing similar carrying capacities within clusters but differences between clusters. The juvenile carrying capacities on reefs within each cluster can be scaled, however, so that there is a linear m -fold variation across these reefs. When $m=1$, $\mathbf{J}_{ij,1}$ was the same for all reefs within each cluster j , and when $m>1$, $\mathbf{J}_{ij,1}$ differed linearly among reefs within each cluster. For example, for 6 reefs with a 3-fold scaling, the carrying capacities of the reefs would vary as follows:

$$5k'/10 \quad 7k'/10 \quad 9k'/10 \quad 11k'/10 \quad 13k'/10 \quad 15k'/10$$

where k' is the mean recruitment capacity of the cluster.

This control allowed us to model explicitly potential systematic differences among reefs locally, without assuming a relationship between dispersal patterns and such systematic variation. Thus, recruitment at the end of the 0+ year was calculated for each reef from:

$$\mathbf{J}_{ij,1} = s_0 * \mathbf{L}_{ij} / [1 + (s_0 * \mathbf{L}_{ij} + \mathbf{JT}_{ij} + \mathbf{A}_{ij}) / (r_{ij} * k')] \quad (\mathbf{A4})$$

where:

$\mathbf{J}_{ij,1}$, s_0 , \mathbf{JT}_{ij} , \mathbf{A}_{ij} , and k' are as defined for (A3); and

r_{ij} = the scaling factor for reef i in cluster j ;

The mechanism used to scale recruitment among reefs within each cluster was the same as that used to scale background larval supply among clusters. Thus, for q reefs to be scaled over an m -fold range, the scaling factor for the i th reef is:

$$r_{ij} = 2[q-1 + (i-1)(m-1)] / [(q-1)(m+1)] \quad (i=1 \dots q).$$

Equations (A0-A4) allow simulation of a great range of population dynamics for reef species. For example, varying the larval retention parameter (ss) in equation A0 allows examination of the effects of local vs global stock-recruitment relationships; decreasing the fecundity*survival parameter (f) reflects increasing risks of recruitment overfishing; and changing k and k' alters how variation in larval abundance influences subsequent abundances of juveniles and adults.

Age Structure & Mortality of Juveniles

Cohorts of juveniles were aged through their 1+ and 2+ years *via* the following survival model:

$$\mathbf{J}_{ij,a+1,y+1} = s_{ij,a,y} * (1-t_j) * \mathbf{J}_{ij,a,y} \quad (\mathbf{A5})$$

where:

$\mathbf{J}_{ij,a,y}$ = the number of juveniles of age a present on reef i in cluster j in year y ;

$\mathbf{J}_{ij,a+1,y+1}$ = resulting juveniles of age $a+1$, on the same reef a year later;

$s_{ij,a,y}$ = age specific annual survival rate in the absence of effects of trawling; and

t_j = mean annual juvenile mortality due to effects of trawling near reef i in cluster j .

Equation (A5) is applied up to an assumed age at maturity y_m , when the cohort enters the adult population \mathbf{A}_{ij} .

Survival at ages 1+ and 2+ were set at 0.6 and 0.7 respectively. Fish were assumed to be adult (reproductively active and of legal catchable size) after their third year post-settlement, and we applied an average annual survival rate of 0.83 to the adult population. This figure was estimated from field data (see main text).

The values for reef-specific survival rates ($s_{ij,a,y}$) were derived from applying a normally distributed inter-annual variation to the mean survival rate at each age, as follows:

$$s_{ij,a,y} = \bar{s}_a * (1 + z_A * \sigma_{sa})$$

where:

z_A = a random normal deviate; and

σ_{sa} = coefficient of variation for mean annual survival rate \bar{s}_a at age a .

Setting $\sigma_{sa} = \sigma_{sa}/\bar{s}_a = 0.05$ results in a 95% confidence region for annual adult survival (0.83) of 0.75-0.91. σ_{sa} is user specified.

Adult Abundance, and Dispersal of Larger Fish Among Reefs

Dynamics of the adult population on reef i in each cluster j (\mathbf{A}_{ij}), allowing for migration of adults among reefs, were modelled with the balance relationship:

$$\mathbf{A}_{ij,y+1} = s_{ij,Ay} * [1 - \mathbf{H}_{ij,y} \mathbf{P}_{ij,y}] * \mathbf{A}_{ij,y} + d * [\bar{\mathbf{A}} - \mathbf{A}_{ij,y}] + \mathbf{J}_{ij,y_m}$$

(A6)

where:

$\mathbf{A}_{ij,y}$ = number of Adults on reef i in cluster j in year y ;

$\mathbf{A}_{ij,y+1}$ = number of Adults on reef i in cluster j in the next year, $y+1$;

$\bar{\mathbf{A}}$ = average abundance of Adults over other reefs in GBR, from which immigration to reef ij might occur;

$s_{ij,Ay}$ = annual natural rate of survival of adults on reef ij in year y ;

- $\mathbf{H}_{ij,y}$ = Annual mortality rate of adults caused by line fishing Harvest on reef ij in year y ;
- $\mathbf{P}_{ij,y}$ = Proportion of adults associated with reef ij susceptible to line fishing in year y ;
- d = average dispersal rate (as a proportion) of adults from each reef in each year y ;
- $\mathbf{J}_{ij,y}$ = number of juveniles entering adult stock on reef ij in year y .

Thus the term $s_{ij,Ay} * [1 - \mathbf{H}_{ij,y} \mathbf{P}_{ij,y}] * \mathbf{A}_{ij,y}$ represents adults on reef ij surviving from the previous year, and $d * [\bar{\mathbf{A}} - \mathbf{A}_{ij,y}]$ gives the net change in abundance of adults on reef ij as a result of expected immigration and emigration. Hence, when fishing depletes population size on a reef it is expected that immigration will outweigh emigration because the abundance of adults on that reef will be less than the average of all (fished & unfished) reefs, but in the absence of fishing on a reef net migration should be off-reef.

Line fishing harvest rate, $\mathbf{H}_{ij,y}$, is depicted as an average exploitation rate, $\bar{\mathbf{H}}$, expected for the all reefs, with a normally distributed stochastic element of variation applied independently at each reef in each year as follows:

$$\mathbf{H}_{ij,y} = \bar{\mathbf{H}} * (1 + z_5 * \sigma_{\bar{\mathbf{H}}})$$

where:

- z_5 = a random normal deviate; and
- $\sigma_{\bar{\mathbf{H}}}$ = the expected inter-annual coefficient of variation of the mean harvest rate.

Both $\bar{\mathbf{H}}$ and $\sigma_{\bar{\mathbf{H}}} (= \sigma_{\bar{\mathbf{H}}} / \bar{\mathbf{H}})$ are user determined parameters. Setting $\sigma_{\bar{\mathbf{H}}} = 0.25$ results in 95% of reef-specific harvest rates lying within a three-fold range. We did not consider any effects of temporal autocorrelation within reefs or spatial correlation among reefs in harvest rate, and we assumed a uniform mean harvest rate over all clusters. Since harvest rates will almost certainly vary regionally and be synchronous among neighbouring reefs, these omissions mean that we implicitly assumed that fishing on the experimental reefs will be deliberately controlled to target levels, though with randomly varying success. We did not

utilise Walters' & Sainsbury's (1990) procedures for simulating the effects of line-fishing harvest over the entire GBR.

Effects of Trawling on Adult Stocks

Habitat disturbance was considered to be the major mechanism by which inter-reef trawling might affect the population dynamics of reef-associated fish and reef-line fishing (Walters & Sainsbury 1990). For example, damage to inter-reef patches of 'reef-like' habitat by trawling would be expected to: i) reduce inter-reef migration by large fish which utilised those patches as stepping stones to other reefs; and ii) reduce the proportion of adults that spent time off-reef (*e.g.*, foraging or spawning) and were thus inaccessible to the reef-line fishery. These effects were modelled by varying the parameters \mathbf{P}_{ij} and d . Hence, inter-reef trawling resulted in reduction in the absolute value of d and increased values of \mathbf{P}_{ij} . As the degree of expected inter-reef migration increased, therefore, inter-reef trawling would result in more variable reef-associated populations that recovered more slowly from experimental increases in line fishing, since the potential for migration to dampen the effects of local recruitment variation and replace fishing losses would have been diminished.

Sampling of Reef Populations

The numbers of juveniles of each age ($\mathbf{J}_{ij,a}$) and adults (\mathbf{A}_{ij}) produced for each reef in each year (=iteration of the model) represented indices of abundance for the whole of each reef. They are, therefore, analogous to estimates of mean per-reef abundances from any field sampling scheme. Such field sampling inevitably would involve taking numerous samples within each reef, usually arranged in some hierarchical sampling design and producing additional uncertainty in the estimates. We depicted that additional 'sampling variation' as an independent, normally distributed effect applied to each abundance index for juveniles ($\mathbf{J}_{ij,a}$) and adults (\mathbf{A}_{ij}). Thus, the sampling variation inherent in the observations of adults on reef i in cluster j in each year was modelled as follows:

$$\hat{\mathbf{A}}_{ij} = \mathbf{A}_{ij} * (1 - z_6 * \mathcal{E}_{obs}) \quad (2.8)$$

where:

$\hat{\mathbf{A}}_{ij}$ = estimated abundance of adults on reef ij ;

\mathbf{A}_{ij} = index of adult abundance on reef ij produced by population dynamics models;

and

z_6 = a random normal deviate;

ϵ_{obs} = the precision (SE/mean) expected from taking *obs* observations per reef.

ϵ_{obs} is set to a value of 0.20 by default, but can be changed by the user to reflect increased or decreased survey effort.

Note that we modelled the estimated abundances for each reef as normally distributed, rather than as log-normally distributed as might be appropriate for the raw count data from sub-samples. We did this because it was expected that each effective replicate datum would be a mean for each reef, calculated from the n' observations (or sub-samples) from that reef. By the central limit theorem, those means would be expected to be normally distributed, with variance MS_w/n' , where MS_w is the highest level Mean Square derived from any hierarchy of sub-sampling within reefs, and n' is the total number of data from which each reef mean is calculated. The value for ϵ_{obs} was derived from empirical data as $\frac{\sqrt{MS_w/n'}}{\bar{R}}$, where \bar{R} is the estimated overall per-reef mean abundance.

APPENDIX 2: Statistical Analyses

The data produced from the simulations were analysed by three methods:

- i. Analyses of Variance (ANOVA) involving annually repeated measures on each reef, in which corrections for autocorrelation among the repeated measurements were calculated and F-tests and contrasts done on the assumption of independent, normally distributed, homoscedastic residuals; and
- ii. the estimation of particular contrasts (mostly between treatment means in each year) between residual values after fitting a simplified General Linear Model to the simulated data.

Analyses of Variance

In the experimental designs described above, line-fishing treatments are to be applied to reefs which are grouped into clusters. Within each cluster there are n ($n=1$ or 2) replicates of each line-fishing treatment. Annual or bi-annual measurements are then made on each reef, although we considered only annual sampling for our simulations. The resulting experimental designs can be described as three factor experiments (Fishing Treatment*Cluster*Time) with repeated measures across the levels of one factor, in this case time. Winer (1971), Winer *et al.* (1992), and Milliken and Johnson (1984) provide detailed discussions of repeated measures designs, and their analysis.

In experiments involving repeated measures on experimental units, the overall residual (or error) variation after accounting for the effects of the factored effects (Fishing Treatment (**F**), Cluster(**C**), Time (**T**) & their interactions) can be divided into two components:

- i. the average variation among experimental units (in this case, variation among reefs(**C*F**));
- ii. the variation among experimental units in their responses to the repeated factor (time) - *i.e.* the interaction between reefs(**C*F**) and time.

A model to describe the estimated densities of fish on each reef in each year, therefore, will generally include two error terms. One such model is:

$$y_{ijk} = \mu + C_{i..} + F_{.j.} + CF_{ij.} + \epsilon_{ijn} + T_{...k} + CT_{i..k} + FT_{.j.k} + CFT_{ij.k} + \tau_{ijnk} + \epsilon_{ijnkm}$$

or

$$y_{ijk} = \mu + \alpha_i + \beta_j + \gamma_k + \delta_{ij} + \epsilon_{jk} + \zeta_{ik} + \eta_{ijk} \text{ (when all } H_0 \text{ true)}$$

where:

y_{ijnk} = observation in year k on reef r in cluster i and subject to treatment j ;

μ = true population mean for all reefs in all years;

$C_{i...}$ = net effect of being in Cluster i

$F_{j..}$ = net effect of Fishing treatment j

$T_{...k}$ = effect of Time, in this case the effect of year k

$CF_{ij..}$, $CT_{i..k}$, $FT_{j.k}$, & $CFT_{ij.k}$ are the departures of y_{ijnk} from μ explained by interactions between the main effects $C_{i...}$, $F_{j..}$, & $T_{...k}$;

$\epsilon_{ijn.}$ = the residual value of $y_{ijn.}$ after subtracting the values $C_{i...}$, $F_{j..}$, & $CT_{ij..}$;

ϵ_{ijnk} = the (non-estimable) residual value of y_{ijnk} after subtracting the values for all other effects and $\epsilon_{ij.}$.

Assuming all factors are fixed effects, the ANOVA for this model would have the form shown in Table A2.

Table A2: Degrees of freedom, parameters estimated by Mean Squares, and F-ratios for repeated measures ANOVAs appropriate to the experimental designs are considered in the body of the report. Cluster, Fishing Treatment, and Time are all assumed to be fixed effects.

Source of Variation	Degrees of Freedom	Mean Square Estimates	F Denom.
Between Reefs			
	$cfr-1$		
Clusters (C)	$c-1$	$\mu^2 + t\epsilon^2 + ftr\epsilon_C^2$	MS_{error}
Fishing Effect (F)	$f-1$	$\mu^2 + t\epsilon^2 + ctr\epsilon_F^2$	MS_{error}
C*F	$(c-1)(f-1)$	$\mu^2 + t\epsilon^2 + tr\epsilon_{CF}^2$	MS_{error}
error (?)	$cf(r-1)$	$\mu^2 + t\epsilon^2$	
Within Reefs			
	$cf(r-1)t$		
Time (T)	$t-1$	$\mu^2 + \epsilon_T^2 + cfr\epsilon_T^2$	$MS_{error(T)}$
T*C	$(t-1)(c-1)$	$\mu^2 + \epsilon_T^2 + fr\epsilon_{TC}^2$	$MS_{error(T)}$
T*F	$(t-1)(f-1)$	$\mu^2 + \epsilon_T^2 + cr\epsilon_{TF}^2$	$MS_{error(T)}$
T*C*F	$(t-1)(c-1)(f-1)$	$\mu^2 + \epsilon_T^2 + r\epsilon_{TCF}^2$	$MS_{error(T)}$
error(T) (T_{\neq})	$cf(r-1)(t-1)$	$\mu^2 + \epsilon_T^2$	

We have treated all factors as fixed effects for the following reasons:

?? Fishing treatments are clearly limited in number and imposed by us. We are interested in the categorical effects of those treatments.

?? Years are sequential (not randomly sampled), the number in which we can work is clearly limited, and each bears a specific relation to the others and to the imposition of the fishing treatments.

?? Clusters are i) limited in number by the availability of neighbouring reefs with a history of closure to fishing; ii) selected to be in specific regions, rather than at random; iii) expected to exhibit responses consistent with gradients in the larval supply and/or recruitment capacity and/or background fishing pressure applied to reefs in the GBR.

In addition to the usual assumptions of ANOVA (homoscedasticity, independent & normally distributed error terms, additivity of effects), the validity of the F-tests for terms involving the repeated measurements (*i.e.* and terms in the above table involving Time), rests on the conditions that: i) the variance-covariance matrices of the within-cell residuals over all times are homogeneous; and ii) that the pooled error variance-covariance matrix over all treatments is spherical. Effectively, these conditions imply that the correlations between residuals from repeated measurements of the same experimental units are homogeneous among experimental units and across all paired combinations of times (repeated measurements) (Winer *et al.*, 1992; Huynh & Feldt 1970).

Strictly, if any of these assumptions are incorrect for a data set, then the ratios of mean-squares calculated will not be distributed as the expected F-distribution, and the results of the statistical analyses are likely to be misleading. Typically, this will mean that the actual probabilities of Type I error will be greater than indicated by the analyses. ANOVA models have been shown to be more robust (=likely to produce correct results) to violation of some assumptions than to violation of others, with homogeneity of variances and covariances (and independence of errors) being more critical than normality of errors (Winer *et al.* 1992, Kendall & Stewart 1979).

If the assumption of homogeneity of the variance-covariance matrix in repeated measures designs is satisfied, then the analyses can proceed as indicated above. It should be expected, however, that the assumption of strict sphericity will be incorrect for many of the variables being measured in the Effects of Fishing project. In these cases, several options are available:

1. Analyse the data from each time separately as a Fishing*Cluster analysis, without the capacity to explicitly examine the effects of time or its interactions with Fishing and/or Cluster;
2. Treat the analyses as a usual repeated measures design but make adjustments to the degrees of freedom for any hypothesis tests involving the repeated factor(s) (in this case time(s)) (Greenhouse & Geisser 1959, Huynh & Feldt 1970);
3. Treat the repeated measurements as multiple variates measured from the same experimental units and analyse the data by Multivariate ANOVA (MANOVA) techniques;
4. Fit an appropriate model to the repeated measurements such that the temporal correlations among errors are removed, and analyse the residual values, after fitting the auto-correlation model (Milliken & Johnson 1984, SAS 1992);
5. Derive the expected distributions of the variance ratios from monte-carlo simulations of data arising under the desired null hypothesis, and compare the observed variance ratios (for the real data) with the empirical distribution rather than with the (assumed) F distribution (Manly 1991).

We adopted strategy 4 for analyses of the simulation data.

ANOVA After Modelling Temporal Error Structure

We expect that the for sequential data from each reef, the residuals in time are likely to have an auto-correlated error structure rather than satisfying the above conditions. This might arise because of a combination of biological mechanisms which cause ‘random’ disturbances to have persistent effects on abundances (*e.g.* survival over many years of unusually strong year classes) and the non-randomization of the time treatment. In such cases the ‘between reef’ analysis (**C, F, C*F**) can be carried out as usual, using the (observed) means over years for each reef (Milliken & Johnson 1984, Winer *et al.* 1992). There is always an exact analysis for the between reefs analysis, irrespective of the presence or absence of autocorrelated errors in time, provided the usual assumptions apply to the behaviour of the reef-means data.

There is no exact within-reef analysis (**T, T*C, T*F, T*C*F**), however, when the temporally separated residuals are not uniformly correlated, and standard tests of these terms are likely to be invalid. Valid approximate tests can be derived for such data by transforming the observations to remove their correlations through time, and analysing the transformed

variables. Several different types of time series models might be appropriate for describing the within-subject (temporal) error structure (see SAS, 1992) and transforming the observations. We considered only a first-order autoregressive [AR(1)] model to remove potential temporal auto-correlation from our simulation data (Milliken & Johnson, 1984), although we recommend exploration of alternative models (SAS 1992) for the future (real) data sets.

Expressing the error(T) term ($\epsilon_{ijk}^2 + \epsilon_{Tijk}^2$) as ϵ_{ijk} , the AR(1) model assumes that the ϵ_{ijk} 's can be expressed as:

$$\epsilon_{ijk} = \rho \epsilon_{ijk-1} + \eta_{ijk}$$

where:

η_{ijk} = independent random normal variates with mean 0 and variance σ^2 for all i, i, k, n ,

ρ = the correlation between successive residuals for each experimental unit; and

ϵ_{ijn0} = independent random normal variates with mean 0 and variance $\frac{\sigma^2}{1 - \rho^2}$ for all $i, i,$

n .

Given this model, Albohali (1983) proposed an approximate transformation to remove the correlation between successive observations. The method uses the maximum likelihood estimate of ρ ($\hat{\rho}$) from the data (Milliken & Johnson 1984, reproduced below) and estimates of ϵ_{ijk} 's ($\hat{\epsilon}_{ijk}$) to 'filter' the data as follows:

$$\hat{\epsilon}_{xijk} = y_{ijk} - \hat{\rho} \hat{\epsilon}_{ijk-1}$$

where:

$$\hat{\epsilon}_{ijk} = y_{ijk} - \bar{y}_{ijn} - \bar{y}_{ij.k} - \bar{y}_{ij..}$$

The within-reefs analysis described above is then done on the filtered data ($\hat{\epsilon}_{ijk}$).

Estimation of the Autocorrelation Factor

As described in Milliken and Johnson (p.367) and modified for the experimental designs we considered, an approximation to the maximum likelihood estimate of ρ is²:

² For calculation of ρ in the GLM analysis (below), the triple sums over i, j, k in the following formulae are replaced with single summations over the number of reefs in the design.

Parameter Estimates from a Simplified Linear Model

Walters and Sainsbury (1990) included in their REEF programme procedures for fitting simplified General Linear Models to the simulation data and estimating the magnitudes of contrasts between treatment effects of interest in each ‘year’, where the year was a reef-specific time relative to the (absolute) year in which the exaggerated fishing treatment was imposed on that reef. They then tested the estimated contrast parameters against a null hypothesis of zero year-specific treatment effect by one-sample t-tests. As Walters & Sainsbury (1990) noted, ‘the GLM model involves statistical assumptions that are more difficult to justify than would simple ANOVA/MANOVA models’. We utilised those procedures to provide consistency between prior treatments of the design problem and this study. The following description of the GLM procedures reflects that offered by Walters & Sainsbury (1990). Detailed treatments of Generalised Linear Modelling can be found in Searle (1971) and Graybill (1979).

Walters’ and Sainsbury’s model treats each observation y (of, for example, abundance of adult coral trout) on reef n in Cluster i with Fishing treatment j at Time (=year) k as follows:

$$y_{ijk} = C_{i...} + CT_{i..k} + FT_{j.k} + ?_{ijk}$$

(G1)

where:

$C_{i...}$ = the time-averaged value of all **unfished** reefs in cluster i ;

$CT_{i..k}$ = the year-specific departure of unfished reefs from C_i , assumed to be common to all reefs in cluster i in year k , but estimated only from the unfished reefs;

$FT_{j.k}$ = the averaged (relative) year-specific effect of fishing treatment j , estimated from all reefs having that treatment in all clusters and assumed to be common to all clusters;

$?_{ijk}$ = reef-specific variation within each cluster i , treatment j , and year k .

As with the ANOVA analysis, the ‘residuals’ ($?_{ijk}$) cannot be assumed to be independent and identically distributed random effects, particularly given that experimental reefs would not be selected strictly at random (see main text). As in the ANOVA model, then, the $?_{ijk}$ are likely to be autocorrelated (see above), and so we ‘filtered’ the data in an attempt to remove the autocorrelation in the residuals:

$$y_{ijk} = y_{ijk} - y_{ijk?}$$

where:

σ^2 is calculated as for the above ANOVA; and

the $\mu_{ijk}^{\tau_1}$ are calculated by fitting the data to the above GLM (*GI*) with $\tau=0$.

The linear model is then fitted again to the 'filtered' data.

From this model of the experimental layout, the REEF programme then estimates the magnitude of those contrasts stipulated by the user. We considered only the contrasts (differences) between the average (over reefs and clusters) for each fishing treatment and the (unfished) controls:

- i. prior to manipulation, to measure the effects of prior fishing on reefs;
- ii. immediately following manipulation, to estimate the capacity of field data to measure the imposed effect;
- iii. each year following closure of reefs after being heavily fished, as an indication of the capacity of the data to convey meaningful information about the 'recovery' dynamics of the protected stocks.

In each case, the estimated difference between treatment and control was compared with zero (the H_0) by a *t*-test based on the standard error of the contrast and having $ncft-p-1$ degrees of freedom, where:

n = number of reefs per treatment per cluster;

c = number of clusters;

f = number of fishing treatments (including 1 control);

t = number of years sampled; and

p = number of parameters estimated.

This approach to the experimental design encapsulates several assumptions which are examined rather than assumed in the ANOVA approach. Specifically, the simplified model above assumes that:

- i. the fishing treatments will affect all reefs in all clusters similarly at any nominated time after manipulation - *i.e.*, there will not be a cluster*treatment*time interaction;

- ii. interactions between fishing treatments and clusters (when averaged over all years) are trivial;
- iii. The main effects of Time and Fishing effects are either trivial (for Time effects) or appropriately considered as contributors to first-order interactions (Fishing).

The assumptions of trivial $C * F$ & $C * F * T$ interactions were generally supported by our ANOVAs of the simulation data, where estimated variances attributable to these terms were consistently trivial or zero ($F < 1$).