

Different responses to area closures and effort controls for sedentary and migratory harvested species in a multispecies coral reef linefishery

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We used a simulation model to examine the effect of area closures and fishing effort on the two main target species of the Great Barrier Reef Coral Reef Finfish Fishery: common coral trout (*Plectropomus leopardus*) and red throat emperor (*Lethrinus miniatus*). Area closures had greater effect on the more sedentary coral trout, in the areas outside the closures and accessible to the fishery, and little effect on red throat emperor, which was assumed to move among reefs. The effects of effort levels were greater than area closures on the harvest of both species and were seen not only in the areas accessible to the fishery, but also in the biomass of red throat emperor in the areas closed to the fishery. The catch and biomass resulting from a given effort level did not appear to have an equivalent effect attributable to any area closure. Although the effects of effort levels and area closures are confounded in reality by the coincidental implementation of area closures and restructuring of the fishery, the simulation model separated these factors to show that the closures under the 2004 rezoning should have had minimal effect on total-stock biomass and that a greater effect would result from changes in fishing effort.

Keywords: effort control, fisheries management, input control, management strategy evaluation, marine protected areas, marine reserves.

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Introduction

Tropical coral reef fisheries are characteristically multispecies, multisectorised, highly patchy, mostly distributed across developing nations (Kritzer and Sale, 2006) and, as a result, difficult to manage. The creation of marine reserves or no-take marine protected areas in which fishing is precluded is currently a popular conservation management strategy (Hilborn *et al.*, 2004), with benefits derived by protecting fish species and habitat (Halpern, 2003). The conservation benefits to populations within areas closed to fishing are well-documented, particularly for less mobile species, and there is belief that marine reserves might benefit fisheries through the spillover of fish from increased biomass within the reserves, resulting in increased catches outside of them (Boersma and Parrish, 1999; Gell and Roberts, 2003).

The Great Barrier Reef (GBR) is one of the largest coral reef ecosystems in the world, with more than 3000 individual coral reefs scattered over >2000 km of coastline. The Coral Reef Finfish Fishery (CRFFF) on the GBR consists of three sectors: a commercial sector, a charter fishing sector that caters to a lucrative tourism industry, and a private recreational sector. The annual

economic value of the CRFFF is ~AU\$60–100 million (Williams, 2002). All sectors use similar gears, consisting of single baited hooks on heavy line with a rod or hand reel. The fishery is multispecies, with more than 125 species groups recorded in the compulsory commercial logbook system managed by the Queensland Department of Primary Industries and Fisheries (QDPI&F; Mapstone *et al.*, 1996). The two main target species are common coral trout (*Plectropomus leopardus*, hereafter referred to as coral trout) and red throat emperor (*Lethrinus miniatus*), which together constitute >65% of the total catch by the commercial sector (Mapstone *et al.*, 1996, 2004, 2008). QDPI&F manage the fishery using seasonal spawning closures, size and hook limits for all sectors, limited entry for the commercial and charter sectors, an individual transferable catch quota (ITQ) system for the commercial sector, and bag limits for the recreational and charter sectors.

The situation is complicated because conservation management within the same area covered by the fishery falls under Australian Federal jurisdiction, with the Great Barrier Reef Marine Park Authority (GBRMPA). The Great Barrier Reef

Marine Park (GBRMP) was established in 1975 to facilitate conservation management, and the Marine Park was included on the World Heritage list as the Great Barrier Reef World Heritage Area (GBRWHA) in 1981. GBRMPA manage the Park primarily through area zoning strategies to conserve and protect biodiversity, and also allow multiple uses, including fishing, in some areas (Day, 2002). No-take zones accounted for some 5% of the total area of the GBRMP and ~24% of the area of the mapped coral reef habitat from the mid-1980s up to mid-2004. A major rezoning programme called the Representative Areas Programme (RAP) was introduced in July 2004 and resulted in no-take zones increasing to 33% of the entire Marine Park and to nearly 40% of coral reef habitat (GBRMPA, 2004; Fernandes *et al.*, 2005).

Understanding of the different fishery sectors and the effects of management actions on the main target species, coral trout, continues to grow (Mapstone *et al.*, 2004, 2008), and knowledge of the other major target species, red throat emperor, has also increased recently (Williams, 2003; Williams *et al.*, 2007a, b). Coral trout and red throat emperor differ in several respects, including rates of growth and natural mortality, but most importantly in the context of this study, in their mobility. Coral trout, for instance, are sedentary, following settlement from an advective larval stage, in demersal reef habitats where they remain for life (Davies, 1995). In contrast, red throat emperor appear to exhibit post-settlement migration among reefs (Williams, 2003). The conservation benefits and fishery implications of closing areas to fishing are therefore likely to differ between the two species.

Simulation modelling of fish populations has been used extensively to understand the general nature of management measures on resources and ecosystems (Sainsbury *et al.*, 2000; Gerber *et al.*, 2003) and, in particular, to examine the relative performance of different options for managing resource exploitation in the medium to long term (Mapstone *et al.*, 2004, 2008; Little *et al.*, 2007). We have developed a multispecies metapopulation model, the Effects of Line Fishing Simulator (ELFSim), to evaluate management options for coral trout and red throat emperor on the GBR (Mapstone *et al.*, 2004, 2008; Little *et al.* 2007, 2008). ELFSim captures the population dynamics of coral trout and red throat emperor along with the dynamics of fishing effort in the CRFFF. We used ELFSim to explore the potential effects of different fishing-effort controls and closing areas to fishing on coral trout and red throat emperor to evaluate the relative effectiveness of spatial and input control measures for species with different post-settlement migration behaviour in the context of a multispecies, multisector, spatially structured fishery.

Methods

ELFSim is a decision-support tool designed to evaluate options for managing the harvest of reef fish species in the CRFFF on the GBR. ELFSim was developed initially to explore the implications of management options for coral trout (Mapstone *et al.*, 2004, 2008; Little *et al.*, 2007), but it has since been updated to include the secondary target species red throat emperor (see the Appendix).

ELFSim operates at a monthly time-step, with each simulation consisting of two parts. The first (initialization) step operates historically from the beginning of the fishery (assumed to be in 1965) to the present (in this case 2003), using information from underwater visual surveys, fishery catch records, and the physical characteristics of the reefs to determine the initial and present size of the population of each species on each reef, allowing for harvest that mimics the reported catches from the fishery. The reef populations

are then projected into the future (projection period) by subjecting them to simulated fishing pressure which is, in turn, influenced by user-specified management regulations. The management regulations available involve area closures, changes to gear selectivity, minimum legal sizes for harvest, the annual allowable fishing effort for each of the fishing sectors (commercial, charter, and recreational) and, more recently, individual quota allocations (Little *et al.*, 2009). Each sector allocates fishing effort spatially and temporally. The model therefore has three key components: a biological model of the fish species, an effort-allocation model related to the exploitation of the resource, and a model that simulates the effects of management measures.

Biological model

Populations of coral trout and red throat emperor are modelled using a spatially explicit age-, size-, and sex-structured model with a monthly time-step and many local post-larval-settlement populations, each associated with a single reef and linked through larval dispersal. Red throat emperor have the additional characteristic that reef-based populations are connected through post-settlement movement, with the age-specific probability of a red throat emperor moving from one reef to another depending on the distance between the source and destination reefs, the size of the destination reef, and the direction of migration [Equation (A4)]. For example, movement is greater between reefs that are close together and large, and between reefs where the destination reef is north of the source reef. Allowance is also made for a maximum monthly movement distance. The probability of moving among reefs increases with age. The northward movement is supported by age data on a latitudinal gradient (Williams, 2003), and observations that the highest densities of juvenile red throat emperor are found in the south of the GBR.

The numbers of larvae (0-year-olds) and recruits (1-year-olds) on each reef depend on the extent of larval dispersal and density-dependence, respectively. The number of 1-year-old fish recruiting to each reef subpopulation each year is determined by the annual total egg production, the assumed pattern of larval distribution among reefs, and density-dependence in first-year survival (Mapstone *et al.*, 2004; Little *et al.*, 2007). Several sources of process error (Francis and Shotton, 1997) are included in the biological model, including variation among reefs and among years in natural mortality and larval supply, and variation in the relationship between fishing effort and fishing mortality. Different models of larval dispersal can be implemented (Little *et al.*, 2007), and we use a model that specifies an inverse relation between the distance from where a larva was spawned and where it settles, parameterized using the output from a hydrodynamic model of the northern GBR (James *et al.*, 2002; Bode *et al.*, 2006). The biological component of ELFSim explicitly allows for a protogynous hermaphroditic life history (as is true for coral trout and red throat emperor; Adams *et al.*, 2000; Adams, 2002; Bean *et al.*, 2003) by making the number of males a size-specific proportion of the total number of fish in each age class, with the proportion of fish of each sex changing with size according to a logistic function.

Simulated fishing pressure and spatial effort allocation

The fishing-effort-allocation model simulates the monthly harvest from each reef during the projection period. It allocates a user-specified total annual effort by each fishing sector to each month according to seasonal patterns observed historically, then distributes the effort for each month spatially (Mapstone *et al.*, 2004;

Little *et al.*, 2007). Seasonality in effort by fishing sector is based on the distribution of effort by month for the years for which data are available (1989–2003 for the commercial fleet, 1996–2003 for the charter fleet, 1999, 2001, 2003 for the recreational fleet). The allocation process for a future year (y) involves selecting a year at random from the appropriate period from which data for each fishery sector exist, calculating the fraction of effort by month for that year, and using these fractions to allocate annual effort to each month for projection year y . The process of allocating monthly fishing effort spatially for the commercial and charter sectors involves: (i) ranking reefs according to a weighted average of catch per unit effort (cpue), where the weights by species are proportional to historical beach prices, then (ii) allocating effort (based on the average effort on the reef historically) from highest to lowest ranks until there is no effort remaining to be allocated. Recreational effort is allocated spatially based on an assumed distribution of recreational fishing effort around the major coastal access points next to the GBR (Mapstone *et al.*, 2004; Little *et al.*, 2007).

Management scenarios

The development of the RAP took place when the reef linefishery was managed primarily through effort control, although bag limits did apply to recreational and charter fishing. The work we report here was carried out in that context. Therefore, simulations were performed using the management options of area closures and fishing-effort controls, which were available to managers at the time the RAP was being developed, although the fishery is now managed mainly through output controls (so ELFSim has been modified to simulate ITQ management and trading).

ELFSim also allows for simulation of infringement into areas closed to fishing by specifying a management status for each reef (Little *et al.*, 2005, 2007), which can vary among reefs depending on the distance to legal fishing areas or the time since the closure was implemented (Little *et al.*, 2005). We used a spatially uniform infringement rate, with closed reefs receiving 5% of any effort that would have been allocated to them had they been open to fishing.

The management scenarios involved three levels of area closure and three levels of total annual fishing effort. Specifically, area closures involved those (i) originally applied from the mid-1980s to mid-2004 (equating to ~16% of reef perimeters on the GBR), (ii) implemented under the rezoning in 2004 (32% of reef perimeters), and (iii) a higher closure regime of 50% of reef perimeters closed to fishing. We used reef perimeter (rather than area) as a measure of closure of fishable ground, because perimeter

is believed to provide a better measure of the habitat of the target species than area enclosed by reef perimeter (Mapstone *et al.*, 2004). Only one candidate spatial configuration for each closure was examined. These were the actual arrangements for the original (16%) and the RAP (32%) situations, and one built by expanding the original configuration to capture 50% of reef habitat (Figure 1). Each of these area closures was combined with three fishing effort levels that were referenced to the effort expended in the fishery in 1996 (the year considered by managers and operators as the one in which the fishery was in a desirable state) and consisted of $0.5 \times$ the 1996 effort level, the 1996 effort level, and $1.5 \times$ the 1996 effort level (Mapstone *et al.*, 1996, 2004).

We used a projection period extending from 2004 to 2025, which allows initial transient dynamics in the harvest model to settle and represents a period for which management and stakeholders have expressed longer-term fishery objectives (Mapstone *et al.*, 2004, 2008). In all, 100 replicate simulations were performed for each scenario combining fishing-effort level and closure regime. These 100 simulations represented a trade-off between the need to capture the stochastic aspects of the model and the intensive computer resources needed to do so. They were based on ten future projections for each of ten initializations of the model, where the replicate initializations captured uncertainty about what was known about the state of the system up to 2004, including initial reef-population densities, and the replicate projections captured variability in population dynamics and effort characterization under each of the alternative management options (Little *et al.*, 2007).

Performance indicators

The performance indicators used to quantify the results of the simulations included the available biomass (the biomass that would be selected by the gear and, if caught, legally retained) as an indicator of the fishable stock size, differentiated between areas open and closed to fishing. The indicators also included the cpue and the commercial harvest to indicate the effect of the management strategies on the fishery.

The results for the different management scenarios were compared based on performance indicators averaged across either open or closed reefs and over the final 5 years of the projection period (2021–2025). We focused on the relative performance of the management options rather than performance in absolute terms. Hence, the values for the performance indicators are reported relative to the management option that is closest to the one operating now, after the introduction of the RAP rezoning of the GBR and following some restructuring of the fishery in

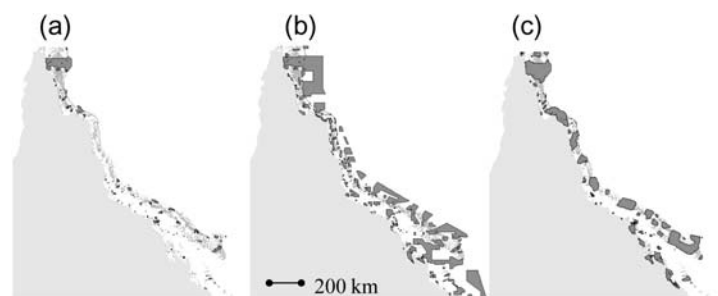


Figure 1. Different area closure scenarios examined in the simulations: (a) 16% area closure, (b) 32% RAP area closures, and (c) 50% area closures. The area closures in ELFSim only counted coral trout and red throat emperor coral reef habitat. The area closures under the RAP include marine habitat that is not coral reef, but covers 32% coral reef habitat, measured by reef perimeter.

2003/2004, hereafter referred to as the *status quo* scenario and comprising $1.0 \times$ the 1996 fishing effort level and 32% area closure.

Results

The biomass in the open areas was inversely proportional to the area closed (Figure 2a). For example, increasing area closures, which reduced the size of the fishable area, led to lower biomass in the open areas than there would have been under the *status quo* management option (Figure 2a). Area closures affected the biomass of sedentary coral trout in the open areas more than they did the migratory red throat emperor. For example, increasing the area closures (i.e. decreasing the fishable area) from 32 to 50% of reef perimeter, while keeping effort at the *status quo* level, decreased the abundance of coral trout that could be taken by the fishery by some 35%, compared with 25% for red throat emperor (Figure 2a). Decreasing the area closures (increasing fishable ground) from 32 to 16% of reef perimeter, while keeping effort at the *status quo* level, increased the biomass of coral trout available to the fishery by $\sim 20\%$ compared with just 15% for red throat emperor (Figure 2a).

The biomass in the closed areas depended not only on the extent of area closed, but also on the quantity of fishing effort that operated outside the closed areas (Figure 2b). The effect of effort on the protected biomass of sedentary coral trout in the closed areas was small, but the effect of effort on the biomass of migratory red throat emperor in closed areas was greater, although there was no (legal) fishing in the closed areas (Figure 2b). For example, under 32% closure, halving the effort resulted in a $\sim 10\%$ increase in coral trout biomass compared with a $\sim 25\%$ increase in red throat emperor biomass on the closed reefs (Figure 2b).

The results for biomass per unit area (Figure 2c and d) showed a slightly different pattern across the open and closed reefs than they did for absolute biomass (Figure 2a and b). For example, although increasing the amount of open area (reducing the area closures to 16%) led to an increase in total coral trout and red throat emperor biomass on the open reefs (~ 20 and 15% , respectively; Figure 2a), the biomass per unit of area actually decreased slightly (~ 4 and 7% , respectively, Figure 2c). This difference was likely attributable to less input coming from the closed areas, in the form of larvae for coral trout and larvae and migrating adults for red throat emperor. In terms of biomass per unit area,

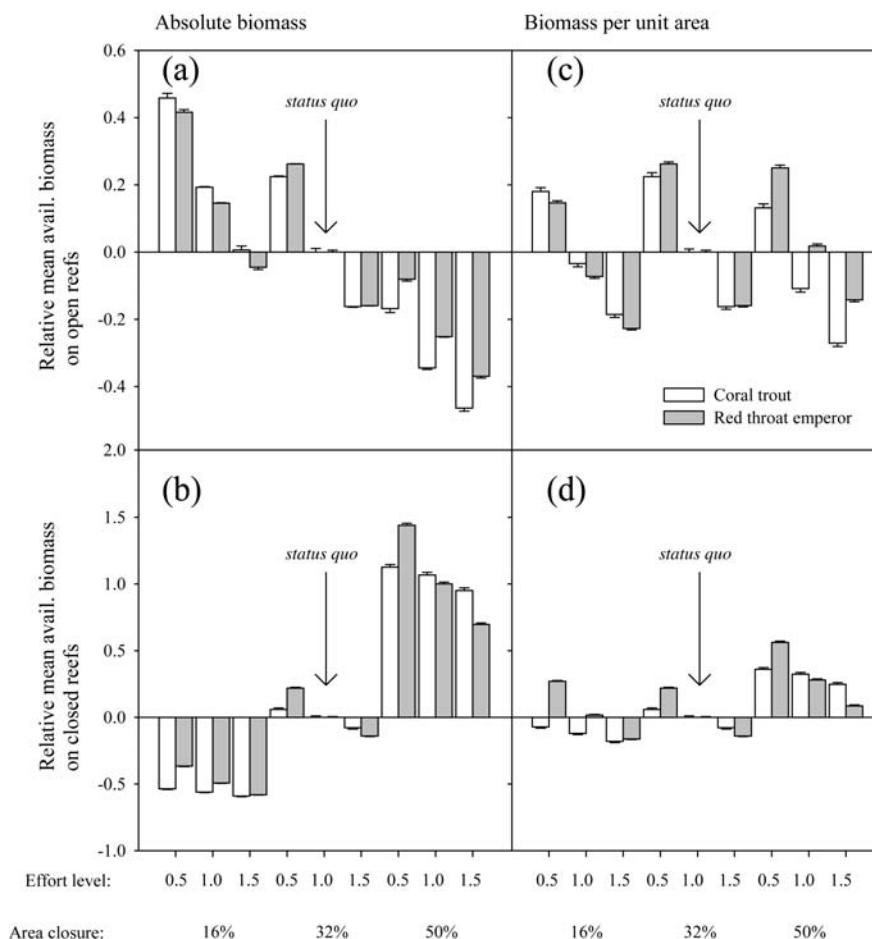


Figure 2. Average (\pm s.e.) available biomass during the final 5 years of simulation (2021–2025) on (a) open reefs and (b) closed reefs relative to mean available biomass (2021–2025) under the *status quo* management strategy (effort level = 1.0, area closure = 32%), and average (\pm s.e.) available biomass per unit area during the final 5 years of simulation on (c) open and (d) closed reefs relative to that under the *status quo* management strategy. Effort expressed is proportional to that in 1996, and area closures are expressed in terms of the fraction of the reef perimeter closed to fishing. Values of relative available biomass are scaled so that 0 equates to no change from the *status quo* result.

the effects of the different scenarios on the reefs closed to fishing (Figure 2d) were noticeably more muted than for absolute total biomass (Figure 2b). For example, reducing the closed area to 16% reduced the absolute biomass of both species by $\sim 50\%$ (Figure 2b), but reduced the sedentary coral trout per unit area in the closed reefs by $\sim 12\%$ and had little effect on the more-migratory red throat emperor (Figure 2d).

The effects of the management options on commercial cpue (Figure 3) generally mimicked those of the biomass in the open areas (Figure 2a and c), in that more fishing effort or larger area closures (less fishing areas) led to lower cpue. The catch rates (Figure 3) tended to mimic the biomass per unit area (Figure 2c) more than the total absolute biomass in the open areas (Figure 2a). Also, the commercial cpue for coral trout tended to be more responsive to increasing closures under a given level of effort than that for red throat emperor (Figure 3), because increasing the area closures led to a greater reduction in coral trout cpue than red throat emperor cpue. Coral trout commercial cpue also tended to be more responsive to changes in effort within a closure regime.

The effects of changing area closures on the commercial harvest differed slightly between species (Figure 4). Increasing closures from 32 to 50% had little effect on the commercial harvest of the more mobile red throat emperor, but led to substantial reductions (by $\sim 20\%$) in the commercial harvest of the more sedentary coral trout (Figure 4). Reducing closures from 32 to 16%, however, increased the harvest of both species by approximately the same proportional amount ($\sim 5\%$). The harvest of both species responded approximately linearly to changes in fishing effort, but more strongly to changes in effort than to changes in area closure.

The trade-offs among the different management strategies between commercial harvest from open reefs and total available biomass, i.e. summed across reefs open and closed to fishing, and used because it is a primary objective of conservation management, showed a strong effect of fishing effort on both species. There was also a conspicuous, though weaker, effect of closing

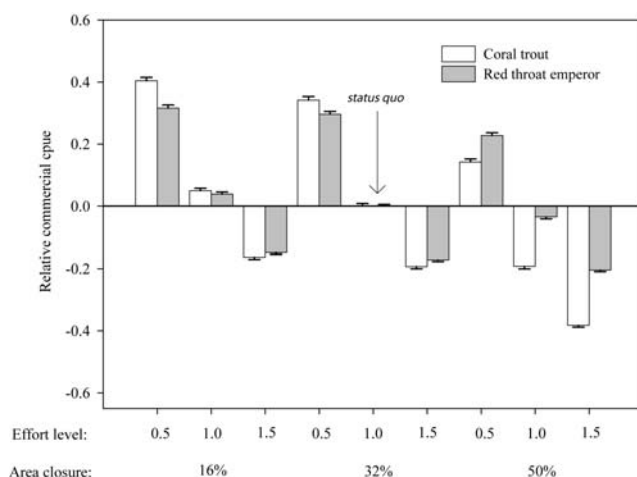


Figure 3. Average (\pm s.e.) commercial cpue during the final 5 years of simulation (2021–2025) relative to mean cpue for the same period under the *status quo* management strategy (effort level = 1.0, area closure = 32%). Values of cpue are scaled so that 0 equates to no change from the *status quo* result.

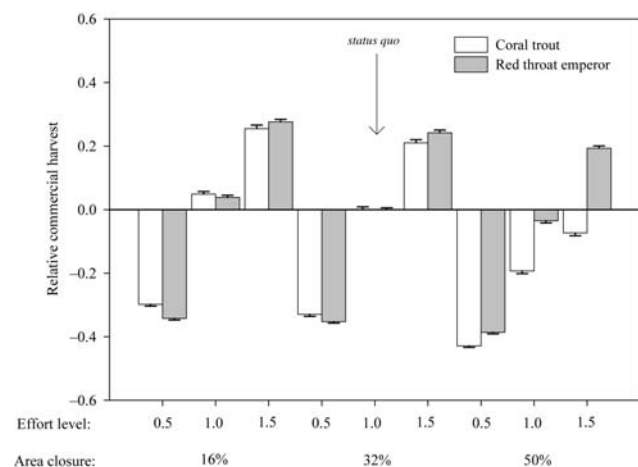


Figure 4. Average (\pm s.e.) commercial harvest during the final 5 years of simulation (2021–2025) relative to the mean commercial harvest under the *status quo* management strategy (effort level = 1.0, area closure = 32%). Harvest values are scaled so that 0 equates to no change from the *status quo* result.

areas to fishing on the biomass and harvest of coral trout. The effect of closing areas to fishing had less of an effect on the more-mobile red throat emperor; increasing closures from 32 to 50%, for example, led to slightly higher biomass, but no discernible effect on harvest.

Discussion

Area closures on the GBR are not implemented to regulate fisheries (action that falls under the state fisheries management agency), but rather as a conservation measure (which falls under the federal jurisdiction of GBRMPA). They are expected to have important fisheries effects, however, because fishing is the primary extractive use on the GBR. Here, we have addressed the complicated issue of measuring the effect and interaction of area closures as a conservation measure with effort controls as a fisheries management measure, in the multispecies, multisector, spatially structured fishery. Computer simulations have shown the effects of changes in fishing effort and area closures. Changing effort did not have the same effect on harvest as changing the relative area closed to fishing, as might be expected (Hastings and Botsford, 1999). For example, halving the area closed from 32 to 16% of the total, which increased the area of fishable habitat by nearly 25%, led to about a 10% increase in harvest of each species. Hastings and Botsford (1999) suggested that a given change in effort level should be equivalent, in terms of catch and biomass, to a similar proportional change in the extent of marine reserves. Such a pattern would lead to intersecting lines in Figure 5, but this did not happen for the range of values that we considered. The reason that the change in area closure was not equivalent to the change in the level of fishing effort, in terms of catch and biomass, is likely the supposed spatially complex nature of the populations and, in particular, the relatively localized dispersal and settlement patterns (Lockwood *et al.*, 2002).

The effect of the various management options depended on each species' ecological characteristics. For example, the effects of increasing area closures on the cpue of the mobile red throat emperor were less than those on the more sedentary coral trout, because red throat emperor that settled in the closed areas

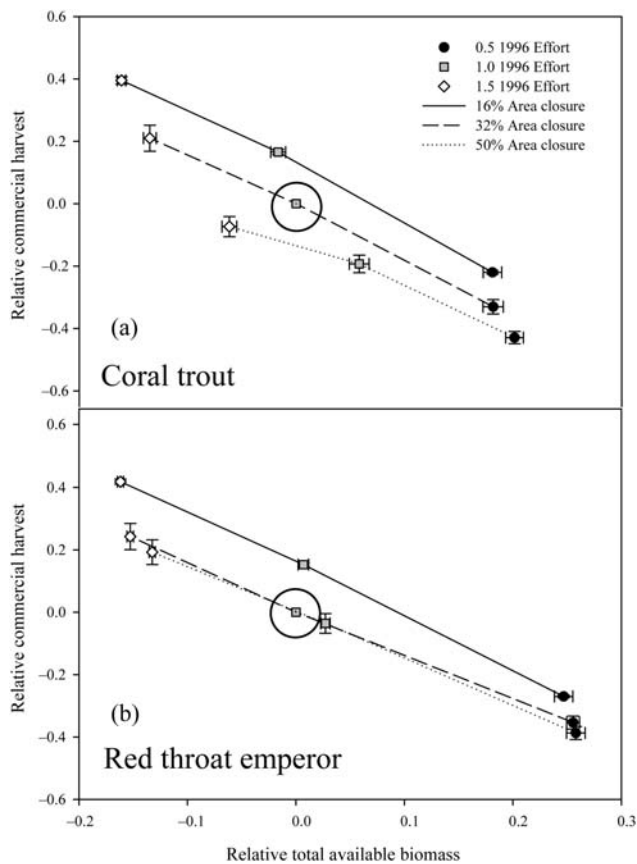


Figure 5. Relative average (\pm s.e.) commercial harvest during the final 5 years of simulation (2021–2025) plotted against the relative total available biomass (available biomass in open and closed areas relative to that under the *status quo* management strategy; effort level = 1.0, area closure = 32%) during the final 5 years of simulation (2021–2025) for (a) coral trout and (b) red throat emperor under the various management strategies. The *status quo* management strategy is circled. Values are scaled so that 0 equates to no change from the *status quo* result.

would move out again and be vulnerable to fishing. For the same reason, effort changes had a greater effect on the biomass of red throat emperor than coral trout on reefs closed to fishing. The small effect of fishing effort on the biomass of coral trout in the closed areas was due to a combination of a slight cost that populations on the closed reefs incur for subsidizing reproduction on the depleted open reefs (Little *et al.*, 2007), as well as the small rate of fishing infringement that was assumed for the closed reefs. In contrast, red throat emperor, which move after settling on a reef, were afforded less protection by closed areas, so the fish in those areas were affected more by the effort operating in the areas open to fishing.

Area closures in our example were less effective on mobile red throat emperor. Area closures can be an effective tool for managing mobile species (Le Quesne and Codling, 2009). However, if the closed areas are a relatively large proportion of the area over which the species moves, if closed areas move with the species (Hyrenbach *et al.*, 2000; Norse *et al.*, 2005), or if critical habitats such as spawning grounds are targeted for closure (Apostolaki *et al.*, 2002; Gell and Roberts, 2003), large and important periods are spent by the fish in protected areas that are largely

unavailable to fisheries. A strategy that could be applied to red throat emperor and examined in the current model would be to concentrate reserves in the southern portion of the GBR, the assumed main spawning area of the species (Williams, 2003; Little *et al.*, 2008).

The two factors of effort and area closures examined are confounded in reality by the coincidental implementation in 2004 of the RAP closures and restructuring of the fishery and introduction of an ITQ management scheme. The effects of the closures within 2 years of their implementation showed that coral trout abundance increased by up to 68% in two of three new inshore marine reserves where fishing had been heavy previously (Russ *et al.*, 2008). New offshore marine reserves displayed significantly greater densities of coral trout than adjacent areas open to fishing, although no data were available to compare the reefs before introduction of the RAP (Russ *et al.*, 2008). Effort in the commercial fishery, however, also declined following the introduction of the RAP, driven largely by new constraints on commercial fishers, industry restructuring, and the introduction of the ITQ scheme, with only some of the existing commercial fishers being allocated quota. With our simulation model, we have teased apart the potential effects of changes in effort and area closures to show that the closures under the 2004 rezoning should have had only a small effect on total-stock biomass and that there would be a greater effect of changes in fishing effort.

Process error in the model is captured in the stochastic treatment of natural mortality and recruitment among individual reefs, as well as the relationship between effort applied to reefs by the harvest model and the catch obtained from the reef (the catchability). The relatively little variability among replicate simulations in the results (the error bars) transpired because the performance indicators we used usually involved summing across all reefs, so inter-reef variability tended to be averaged out.

Species interactions, either ecologically or through differential targeting by the fishery, were not addressed in our model because the extent of ecological interaction is not well known or is thought to be weak. Moreover, we did not model individual fisher behaviour, so could not model differential targeting dynamics explicitly. The possibility that these results are influenced by the choice of harvest model has been considered. We believe that the fishing-effort-allocation model is a plausible representation of reality because previous work has compared model output from it to that of an individual-based model of fisher behaviour (Little *et al.*, 2008), with little apparent qualitative difference. The development of an individual-based model of fisher behaviour has continued, however, with vessel characteristics including variable costs associated with exploiting different reefs and species-specific targeting being used to capture the response to output management controls (Little *et al.*, 2004, 2009).

Although management has been implemented using output controls in the fishery in the form of an ITQ system, our results continue to apply to the CRFFF because the closure and effort conditions experienced in the fishery continue to be within the bounds we considered. For example, effort in the fishery peaked in 2002/2003, at about 50% more than the 1996 effort, but it since dropped to about half the 1996 level by 2007 (Anon., 2007), whereas the closures under the RAP continue. Nevertheless, the results we have presented show, from a more general perspective, that ecological characteristics, including species mobility, are important factors when evaluating the

effects of marine reserves as a tool for natural resource management.

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Appendix: The Biological Model

Basic dynamics

The basic population dynamics are defined by the equations:

$$N_{y+1,a}^r = \begin{cases} \tilde{N}_{y+1,0}^r & a=0 \\ \sum_{r'} T_{a,r,r'}^r N_{y+1,1}^{r'} & a=1 \\ \sum_{r'} T_{a-1,r',r}^r N_{y,12,a-1}^{r'} e^{-Z_{y,12,a-1}^{r'}} & a=2, \dots, x-1 \\ \sum_{r'} (T_{x-1,r',r}^r N_{y,12,x-1}^{r'} e^{-Z_{y,12,x-1}^{r'}} + T_{x,r',r}^r N_{y,12,x}^{r'} e^{-Z_{y,12,x}^{r'}}) & a=x, \end{cases} \quad (A1)$$

where $N_{y,a}^r$ is the number of fish of age a on reef r at the start of year y , $N_{y,m,a}^r$ the number of fish of age a on reef r at the start of month m of year y (by definition $N_{y,1,a}^r = N_{y,a}^r$):

$$N_{y,m+1,a}^r = N_{y,m,a}^r e^{-Z_{y,m,a}^r}, \quad (A2)$$

$Z_{y,m,a}^r$ the total mortality on fish of age a on reef r during month m

of year y :

$$Z_{y,m,a}^r = \frac{M_{y,a}^r}{12} + \sum_f F_{y,m,a,f}^r, \quad (A3)$$

$M_{y,a}^r$ the instantaneous rate of natural mortality on fish of age a on reef r during year y , $T_{a,r,r'}^r$ the probability that a fish of age a on reef r' moves to reef r , $F_{y,m,a,f}^r$ the fishing mortality on fish of age a on reef r during month m of year y by fishery sector f (0, commercial; 1, charter; 2, recreational), and x the maximum age considered (taken to be a “plus group”). The maximum age x for each species (18 years for coral trout, 15 years for red throat emperor; Table A1) has little effect on the results, because the average rate of natural mortality (0.45 year^{-1} for coral trout, 0.40 year^{-1} for red throat emperor; Table A1) assumed for fish aged 2 years and older implies that very few fish attain age x .

There is no movement of coral trout post-settlement, so the matrix \mathbf{T} for coral trout is an identity matrix. The age-specific probability of a red throat emperor moving from reef r' to reef r is

$$T_{a,r,r'}^r = \begin{cases} \frac{\alpha_T P_a S_r S_{r'}}{C + D(r-r')} \left[\lambda_1 + \frac{1-\lambda_1}{1 + \exp(-(L_r - L_{r'})\lambda_2)} \right] & \text{if } r \neq r', D(r-r') \leq \tilde{D} \\ 0 & \text{if } r \neq r', D(r-r') > \tilde{D} \\ 1 - P_a & r = r' \end{cases}, \quad (A4)$$

where $D(r_1 - r_2)$ is the square of the distance (in degrees) between reefs r_1 and r_2 , \tilde{D} the square of the maximum distance a fish can travel in a month (in degrees), C a scaling constant, S_r a measure of the size of reef r (i.e. reef perimeter), P_a the relative probability that a fish of age a migrates from a reef:

$$P_a = \chi P_\infty + \frac{(1-\chi)P_\infty}{1 + \exp(-(a-\phi)\delta)}, \quad (A5)$$

P_∞ the maximum rate of movement, χ a parameter that determines the default level of diffusion, ϕ , δ parameters that determine how the movement rate changes with age a , L_r the latitude of reef r , λ_1 a parameter that allows for a default level of movement, λ_2 a parameter that allows for directed (northward) migration, and α_T is a scaling parameter such that

$$\alpha_T = \frac{1}{\sum_{r' \neq r} (P_a S_r S_{r'} / (C + D(r-r'))) \left[\lambda_1 + (1-\lambda_1) / (1 + \exp(-(L_r - L_{r'})\lambda_2)) \right]} \quad \text{for } D(r-r') \leq \tilde{D}. \quad (A6)$$

Table A1. Values for the parameters of the biological model for coral trout and red throat emperor.

Parameter	Symbol	Coral trout	Red throat emperor	Source
Maximum age	x	18 years	15 years	Mapstone <i>et al.</i> (1996) and Williams (2003)
Natural mortality-at-age ($a > 2$)	M_a	0.45 year^{-1}	0.40 year^{-1}	Little <i>et al.</i> (2008)
Temporal variation in natural mortality	σ_M	0.05	0.05	Mapstone <i>et al.</i> (1996)
Larval self-seeding	st	0.1	0.1	Assumed
Steepness	h	0.5	0.5	Assumed
Variation in 0-year-old survival	σ_r	0.6	0.6	Mapstone <i>et al.</i> (1996)
Spatial correlation in 0-year-old survival	τ_r	0.5	0.5	Assumed
Fraction of fish that die after being released	D'	0.15	0.15	Assumed

Births and recruitment

Red throat emperor are thought to spawn in a more restrictive geographic range than coral trout (Williams, 2003). This is modelled by assuming that there is an ideal latitude for settlement and that the number of 0-year-old red throat emperor declines with distance from this latitude:

$$\tilde{N}_{y,0}^r = \begin{cases} N_{y,0}^r e^{-(L_r - \bar{L})^2 / (\sigma_1)^2} & \text{if } L_r \leq \bar{L} \\ N_{y,0}^r e^{-(L_r - \bar{L})^2 / (\sigma_2)^2} & \text{otherwise,} \end{cases} \quad (\text{A7})$$

where $N_{y,0}^r$ is the expected number of larvae settling on reef r

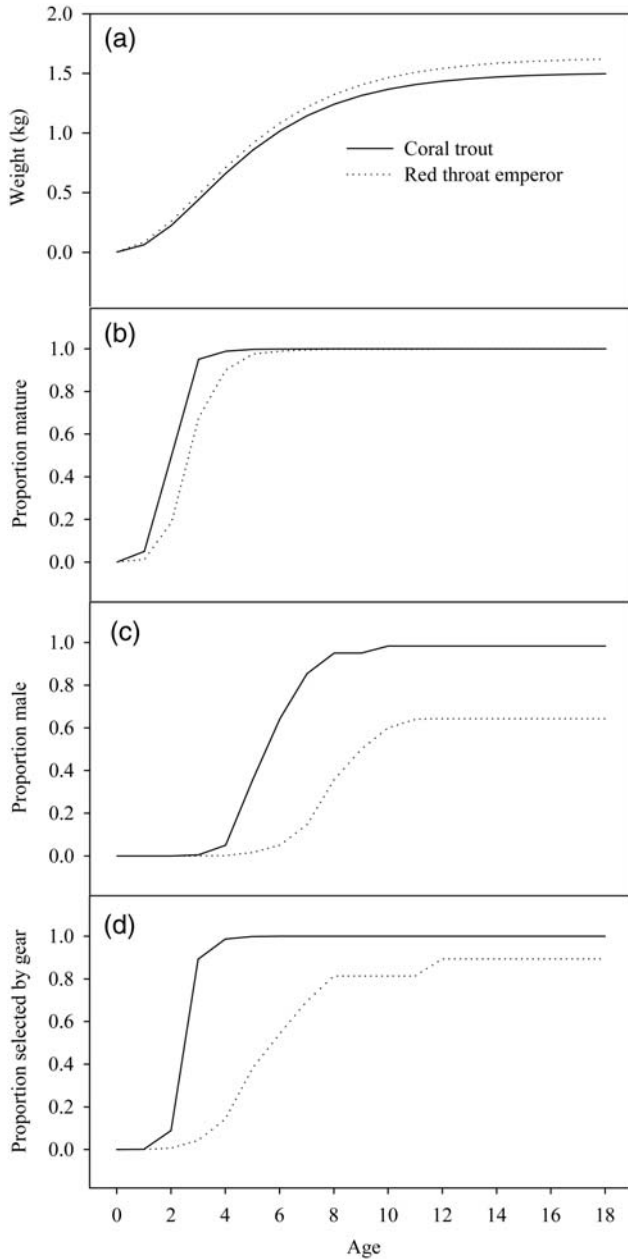


Figure A1. Age-specific biological and fisheries characteristics of coral trout and red throat emperor used in ELFSim: (a) weight, (b) proportion of the population that is mature, (c) proportion of the population that is male, and (d) proportion of the population that is selected by the fishing gear.

during year y :

$$N_{y,0}^r = N_0^r \left[\frac{\text{st } S_y^r}{S_0^r} + \frac{(1 - \text{st}) \text{BL}_y^r}{\sum_{r' \neq r} (N_0^{r'} \Omega_{r',r})} \right], \quad (\text{A8})$$

\bar{L} is the latitude at which 0-year-old density peaks, σ_1 determines the rate at which 0-year-old density drops off with decreasing latitude, σ_2 determines the rate at which 0-year-old density drops off with increasing latitude, N_0^r is the number of 0-year-olds on reef r at pre-exploitation equilibrium, st the fraction of larvae that settle on reef r that originated from reef r , S_0^r the size of the reproductive component of the population on reef r at pre-exploitation equilibrium, S_y^r the size of the reproductive component of the population on reef r at the start of year y (taken to be the biomass of mature females—also referred to as the spawning biomass):

$$S_y^r = \sum_{a=1}^x f_a w_a N_{y,a}^r (1 - \tilde{P}_a), \quad (\text{A9})$$

w_a the mass of a fish of age a (Figure A1a), f_a the fraction of fish of age a that are mature (Figure A1b, derived from a logistic function of length), \tilde{P}_a the fraction of fish of age a that are male (Figure A1c, derived from a logistic function of length), BL_y^r the background supply of larvae to reef r from all reefs except reef r during year y :

$$\text{BL}_y^r = \sum_{r' \neq r} \frac{\Omega_{r,r'} N_0^{r'} S_y^{r'}}{S_0^r}, \quad (\text{A10})$$

and $\Omega_{r,r'}$ is the fraction of larvae that move from reef r' to reef r , $r' \neq r$.

The number of 1-year-olds on reef r at the start of year y is the number of 0-year-olds on reef r during the previous year modified by the density-dependent mortality between ages 0 and 1, plus a component that captures spatially-correlated lognormal environmental variability in larval survival (which effectively allows for occasional spatially-correlated recruitment pulses characteristic of many reef fish species):

$$N_{y,1}^r = N_{y-1,0}^r e^{-M_{y-1,a}^r - \beta_r (U_y^r / U_0^r - 1)} e^{\varepsilon_{y-1}^r - \sigma_r^2 / 2}, \quad (\text{A11})$$

$$U_y^r = N_{y-1,0}^r e^{-M_{y-1,0}^r} + \sum_{a=2}^x N_{y,a}^r, \quad (\text{A12})$$

$$\varepsilon_{y-1}^r = \tau z_{y-1} + \sqrt{1 - \tau^2} z_{y-1}^r; \quad (\text{A13})$$

$$z_{y-1} \sim N(0, \sigma_\tau^2), \quad z_{y-1}^r \sim N(0, \sigma_r^2),$$

where β_r is the density-dependence parameter for reef r , U_y^r the total number of fish aged 1 and older on reef r at the start of year y , U_0^r the value of U_y^r at pre-exploitation equilibrium, ε_y^r is drawn from a bivariate normal distribution, with correlation τ , representing the variation in recruitment specific to each individual reef, and the variation in recruitment common to all reefs, and σ_r^2 is the overall interannual variation in larval abundance. The value of β_r is determined from the “steepness” of the stock–recruitment relationship, h (see Appendix to Little *et al.*, 2007). Steepness is defined after Francis (1992) to be the fraction of the (average) pre-exploitation number of 1-year-olds expected when the spawning biomass is reduced to 20% of its (average) pre-exploitation level. The use of a Ricker-like relationship (Ricker, 1954) for the mortality between ages 0 and 1 in Equation (A11) is based on the assumption that this mortality

is attributable to competition between settling animals and the 1+ population already on the reef.

Natural mortality

Allowance is made for differences in the mean value of natural mortality among ages and reefs, and variability in natural mortality among years:

$$M_{y,a}^r = M_a e^{\varepsilon_{My,a}} e^{-(\sigma_M)^2/2} \quad \varepsilon_{My,a} \sim N(0; (\sigma_M)^2), \quad (A14)$$

where M_a is the expected rate of natural mortality for a fish of age a , and σ_M determines the temporal variation in natural mortality.

Catches

The retained catch (by weight) of fish from reef r during month m of year y by fishery sector v , $C_{y,m,v}^r$ is computed using the equations

$$C_{y,m,v}^r = \sum_{a=0}^x \frac{w_{a+0.5} F_{y,m,a,v}^r}{Z_{y,m,a}^r} N_{y,m,a}^r (1 - e^{-Z_{y,m,a}^r}), \quad (A15)$$

$$F_{y,m,a,v}^r = \begin{cases} D' V_{a+0.5} F_{y,m,v}^r & \text{if } L < L_{MLS} \\ V_{a+0.5} F_{y,m,v}^r & \text{otherwise,} \end{cases} \quad (A16)$$

where D' is the fraction of fish that die after being released, L_{MLS} the minimum legal size, V_a the selectivity of the gear on fish of age a (Figure A1d, derived from a logistic function of length), and $F_{y,m,v}^r$ the fully selected fishing mortality applied to reef r by fishery sector v during month m of year y .

The fishing mortalities by which fish are removed from the population are calculated differently in the historical and projection periods. Fishing mortality during the historical period is calculated based on known catches and the predicted population age structure by solving Equations (A15) and (A16) for $F_{y,m,v}^r$. Fishing mortalities in the projection period are calculated from the monthly effort by reef and fishery sector using the equation

$$F_{y,m,v}^r = q_v^r E_{y,m,v}^r e^{\varepsilon_{y,m,v}^r} e^{\sigma_{q_v}^2/2} \quad \varepsilon_{y,m,v}^r \sim N(0; \sigma_{q_v}^2), \quad (A17)$$

where $E_{y,m,v}^r$ is the effort applied by fishery sector v on reef r during month m of year y , $\sigma_{q_v}^r$ determines the random variation in catchability on reef r by fishery sector v , and q_v^r is the average catchability coefficient for fishery sector v and reef r .

Initial conditions

The population is assumed to have been at pre-exploitation equilibrium with the corresponding age- and sex-structure at the start of 1965. The population sizes (of coral trout) and the corresponding age- and sex-structures on each reef at the start of the 1965 are computed based on the densities for unfished reefs (see Little *et al.*, 2007, for full details).

Parameterization

The parameters of the population dynamics model (Table A1, Figure A1) are based on analyses of biological data for coral trout and red throat emperor. The parameters describing the movement of red throat emperor were determined by fitting

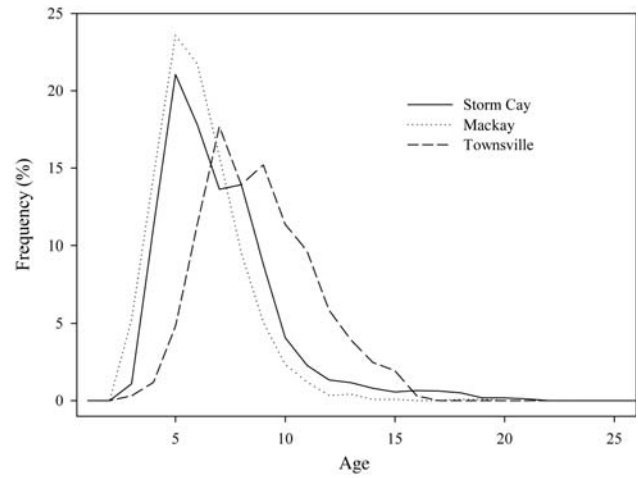


Figure A2. Red throat emperor age structures observed at Storm Cay, Mackay, and Townsville (after Williams, 2003).

Equations (A5) and (A6) to age data for three regions (Φ) of the GBR (Storm Cay, Mackay, and Townsville; Figure A2; Williams, 2003) under the assumption of constant recruitment. The model was also fitted to the observed mean weight and catch rate in these regions (Table A2). The maximum distance that a fish could travel in a month was based on recent tag-recapture studies showing maximum distances travelled of ~ 20 km in a period of 6–24 months (W. Sawynok, Infofish, unpublished data; Williams, 2003). The analyses were based on the fastest rate from this range (20 km in 6 months), which led to a maximum distance a fish could travel in a month of 0.034, or ~ 3.4 km per month.

The negative log-likelihood minimized to determine the values for the free parameters of the post-settlement model for red throat emperor is

$$\lambda = \sum_{\Phi} 0.5 \left[\frac{1}{k_{\text{weight}}} \ln \left(\frac{W^{\Phi}}{\hat{W}^{\Phi}} \right) \right]^2 + \sum_{\Phi} 0.5 \left[\frac{1}{k_{\text{cpue}}} \ln \left(\frac{U^{\Phi}}{q \hat{U}^{\Phi}} \right) \right]^2 - 100 \sum_{\Phi} \sum_a \rho_a^{\Phi} \ln \left(\frac{\hat{\rho}_a^{\Phi}}{\rho_a^{\Phi}} \right), \quad (A18)$$

where k_{weight} was set to 0.2, W^{Φ} the observed mean weight of a fish in region Φ (Table A2), \hat{W}^{Φ} the model estimate of the mean weight of a fish in region Φ :

$$\hat{W}^{\Phi} = \frac{1}{\hat{U}^{\Phi}} \sum_{a_k} \hat{\rho}_a^{\Phi} S_a w_a^{\Phi}, \quad (A19)$$

w_a^{Φ} the weight of a fish of age a in region Φ , ρ_a^{Φ} the observed fraction of the animals in region Φ that are of age a , $\hat{\rho}_a^{\Phi}$ the model estimate of the fraction of the animals in region Φ that are of age a :

$$\hat{\rho}_a^{\Phi} = \frac{\sum_{r \in \Phi} V_a N_{y^*,12,a}^r}{\sum_{r \in \Phi} \sum_{a'} V_{a'} N_{y^*,12,a'}^r}, \quad (A20)$$

y^* the final period of the model, k_{cpue} the coefficient of variation for the catch-rate data and set to 0.2, U^{Φ} the observed catch rate in region

Φ (Table A2), \hat{U}^Φ the model estimate of the catch rate in region Φ :

$$\hat{U}^\Phi = \sum_{a_k}^x \hat{\rho}_a^\Phi S_a, \quad (\text{A21})$$

a_k the minimum age of fish retention (age 2), and q the catchability coefficient.

The resulting migration parameters are given in Table A3. The model estimated only a one-tail distribution in recruitment, because movement was assumed only in a northward direction. Note that the parameters of Equations (A5) and (A6) are only provided for red throat emperor because coral trout are assumed not to move.

Table A2. Regional data for fitting the post-settlement migration parameters.

Region (Φ)	W^Φ	U^Φ
Townsville	1.4489	0.0388
Mackay	1.2684	0.0481
Storm Cay	1.2812	0.0499

Table A3. Estimated post-settlement migration parameters for red throat emperor.

Parameter	Symbol	Value
Latitude at which 0-year-old density is maximized	\bar{L}	21.3
Rate at which 0-year-old density drops off with decreasing latitude north	σ_1	0.19
Rate at which 0-year-old density drops off with increasing latitude south	σ_2	1000
Constant	C	0.44
Maximum rate of movement	P_∞	0.99
Parameter that determines the basal level of diffusion	χ	0.29
Parameter that governs how the movement rate changes with age	a_{50}	0.97
Parameter that governs how the movement rate changes with age	δ	0.12
Basal level of diffusion	λ_1	4.8×10^{-6}
Parameter that allows for the extent of directed (northward) migration	λ_2	6.49

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