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Exploitation and movements of yellowfin tuna (*Thunnus albacares*) and bigeye tuna (*T. obesus*) tagged in the north-western Coral Sea

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Abstract. Yellowfin tuna (*Thunnus albacares*) and bigeye tuna (*T. obesus*) were tagged and released in the north-western Coral Sea off northern Queensland in 1991 and 1992. Over the next five years, recaptures were reported by Australian longline vessels based in Cairns and fishing in the release area, and by industrial tuna fleets fishing in the adjacent western Pacific region, thus demonstrating clear links between the tuna stocks in these areas. Some southerly movements of yellowfin, in particular, further suggested links with stocks supporting the longline fishery in the south-eastern Australian Fishing Zone.

Bigeye tuna tag returns and catch per unit effort by Cairns-based longliners showed a strong seasonal signal, peaking in mid year. Yellowfin tag-return data displayed a similar, but weaker, seasonal pattern. The data were analysed by use of tag-attrition models with seasonally variable catchability and with two assumptions regarding changes in targeting of the two species by longliners during the study. Under both assumptions, the local exploitation rates for yellowfin are low: about 0.07 in 1996. For bigeye, the local exploitation rate in 1996 may have been as high as 0.30, warranting a cautious approach to further fishery expansion in this area.

Introduction

Yellowfin tuna (*Thunnus albacares*) and bigeye tuna (*T. obesus*) are the largest components of the catch of Australian and Japanese longline fisheries operating in the Australian Fishing Zone (AFZ) between Cape York and south-eastern Tasmania. Although small by international standards, the domestic Australian fishery is lucrative, because most of its catch is sent fresh to the Japanese sashimi market. Although Japanese longliners have been fishing in the region since the 1950s (Suzuki *et al.* 1978), the domestic fishery began only in the mid 1980s after the demise of the New South Wales southern bluefin tuna (*T. maccoyii*) fishery. Today, it involves a large number of small operators scattered along the length of the east coast.

Annual catches of yellowfin in the eastern AFZ have ranged from several hundred tonnes to almost 5000 t since 1979, with an average of 28% of the catch being taken by the Australian fleet since 1987. Annual bigeye catches are <1000 t, and an average of 8% was taken by the Australian fleet in the years before 1995. Since 1995, the catch of both species by Australian longliners has increased with the expansion of the Cairns-based fleet fishing in the north-western Coral Sea and the start of a domestic longline fishery off southern Queensland.

Throughout the broader western Pacific region, yellowfin, bigeye and skipjack (*Katsuwonus pelamis*) are caught in one of the world's largest fisheries. In 1994, ~380 000 t of yellowfin, 53 000 t of bigeye and 850 000 t of skipjack were harvested in commercial fisheries across the western Pacific, including the seas around the Philippines and eastern Indonesia (Lawson 1995).

The relationship between the large stocks of tunas in the western tropical Pacific (WTP) and those in the eastern AFZ is unknown. Some authors have speculated that yellowfin spawning in the north-western Coral Sea may ultimately be a major source of recruits to the longline fishery in the eastern AFZ (Anon. 1989; McPherson 1991), while others have suggested that the broad pool of recruits produced in the WTP may be the source (Gunn and Ward 1994). Studies of genetic differentiation among yellowfin tuna caught at widely separated sites across the eastern, central and western Pacific Ocean (including the AFZ) found significant spatial heterogeneity on one allozyme locus between fish caught in the central and western Pacific and those caught in the eastern Pacific (Ward et al. 1994). There was no significant heterogeneity in either allozyme loci or mtDNA among sites in the WTP, nor between fish collected in the AFZ and other parts of the WTP. Ward et al. (1994) interpreted their data as indicating two reproductively isolated populations - one in the eastern Pacific, the other in the central and western Pacific.

Although tagging studies across the WTP have shown that yellowfin can migrate more than 1000 n.miles, most (~90%) tag returns from the 1990–92 Regional Tuna Tagging Project (RTTP) of the South Pacific Commission (SPC) have been within 1000 n.miles of the point of release (South Pacific Commission, unpublished), a pattern consistent with a degree of regional fidelity.

Bigeye have been assumed, principally on the basis of indirect evidence, to belong to a Pacific-wide stock, without the partitioning between eastern and central-western regions recognized for yellowfin (Miyabe 1994). RTTP data for bigeye (which are fewer than the yellowfin data) show similar movement patterns to those of yellowfin: some long-distance movements, but with most recoveries near their release sites.

Yellowfin were first tagged in Australian waters in 1979, when the SPC Skipjack Survey and Assessment Program tagged 322 yellowfin in the Coral Sea. Only one was recaptured, close to its point of release (Itano and Williams 1992). The same program tagged more than 9000 yellowfin over a broad area of the WTP; one fish tagged in the south-east Solomon Islands was recaptured in the Coral Sea, east of Cairns but outside the AFZ. In 1986, 1400 yellowfin were tagged along the east Australian coast (Anon. 1989); 34 were recaptured, mostly along the New South Wales coast within 200 n.miles of release. The longest straight-line distance between release and recapture was 569 n.miles after 9 months at liberty. Gamefishers have also tagged and released 12000 yellowfin in a programme run by the NSW Fisheries Research Institute. From these releases, 273 recaptures have been reported; most were within the AFZ less than 600 n.miles from their points of release.

Bigeye were also tagged in Australian waters in 1986, 66 in the Coral Sea. Of these, five were recaptured: three in the Coral Sea a year after release and two >2500 n.miles to the east in the central Pacific 2.5 and 3.5 years after release (Miyabe 1994).

In 1991, growing interest in the structure of yellowfin and bigeye stocks exploited in the eastern AFZ, and the need to know how they are related to the large stocks of the WTP, prompted CSIRO and SPC to extend the RTTP into the northwestern Coral Sea. During the October and November fullmoon periods, yellowfin and bigeye aggregate in the northwestern Coral Sea off Cairns, in association with large spawning aggregations of the lanternfish *Diaphus* sp. (McPherson 1988). These tuna aggregations had been fished for some years by Japanese longliners, which would change to handlining during the full-moon periods because the fish became vulnerable to surface baits and chumming (the throwing of live or dead bait into the water in order to stimulate feeding behaviour of the target fish). The availability of surface-orientated and essentially stationary schools of tuna was seen as a good opportunity to tag a large number of fish. Following the success of the October–November 1991 tagging operation, additional tagging was undertaken in November 1992.

This paper presents an analysis of recoveries of bigeye and yellowfin tuna tagged in the north-western Coral Sea in 1991 and 1992. We fit a simple tag-attrition model with seasonally variable catchability to the tag returns by the Cairns-based Australian longliners fishing in the study area. We use the results of the model and other data to discuss local exploitation patterns and the possible relationship between yellowfin and bigeye tuna in the study area and those of the WTP.

Materials and methods

Study area

Fish were tagged in the north-western Coral Sea, within $14^{\circ}-20^{\circ}$ S and $14^{\circ}-153^{\circ}$ E (Fig. 1). Since the 1950s, around the October and November full moons, this area has been targeted by Japanese longliners using handlines to catch yellowfin and bigeye tuna (Hisada 1973). Over the past several years,



Fig. 1. Study area in the north-western Coral Sea, showing release sites of tagged bigeye and yellowfin tuna in 1991 (open circles) and 1992 (shaded circles). Each circle represents a fishing episode; the area of a circle is proportional to the number of tuna tagged.

this area has also been the core operational area for the Cairns-based Australian longline fleet.

Tag releases

Tagging was carried out from the MFV *Te Tautai*, a 39.2 m, 173 gross t, Japanese-style pole-and-line vessel. The *Te Tautai* was used throughout the RTTP, in which over 150 000 yellowfin, bigeye and skipjack were tagged in the WTP. The methods used for tagging in the Coral Sea are described in detail by Itano and Bailey (1991).

When schools or aggregations were detected, the tuna were attracted to the tagging vessel with live bait, predominantly *Spratelloides gracilis*, *S. lewisi* and *Encrasicholina devisi*. With the exception of one evening, when fishing continued after dark, all fishing took place in daylight hours. For the aggregations, which tended to be either stationary or moving very slowly, tuna, once attracted to the boat, were chummed (stimulated to feed) with either larger live bait (*Herklotsichthys quadrimaculatus*) or dead bait (*Sardinops neopilchardus* and *Scomber japonicus*), or a combination of the two.

Short (6–14 m) handlines of knotted cord with a nylon leader were used to hook and land fish. The handlines were fitted with barbless feather jigs or baited hooks. Fish were landed onto either tagging cradles or mattresses with smooth vinyl surfaces. The length (nearest cm) of each tagged fish was recorded and a single 13 cm yellow Hallprint dart tag was inserted into the dorsal musculature about half way between the anterior and posterior insertions of the second dorsal fin.

Tagging took place in October–November 1991 and November 1992. In 1991, large aggregations of yellowfin and bigeye tuna were found close to Bougainville Reef in the north-western section of the study area. The aggregations were associated with large numbers of small petrels and whale sharks, and most fish caught had stomachs full of lanternfish. In all, 6227 tagged bigeye and yellowfin tuna were released (Table 1). In 1992, despite extensive searches throughout the study area, no aggregations were found. Mixed schools of yellowfin and bigeye were sometimes found on the surface, but these were all moving schools, which were feeding on the oceanic anchovy, *Stolephorous punctifer*. As a result, only 955 tagged bigeye and yellowfin tuna were released (Table 1). Of these, 73 yellowfin and 105 bigeye tuna were injected with 250 mg g⁻¹ strontium chloride solution for age validation.

The bigeye tagged in 1991 were caught in 21 'fishing episodes' and in 1992 from 5 'fishing episodes' (a 'fishing episode' is defined as a group of tuna fished at the same site at about the same time). The yellowfin were caught in 35 episodes in 1991 and 8 in 1992. The spatial distribution of releases is shown in Fig. 1.

The tagged bigeye and yellowfin ranged in size from 42 to 140 cm fork length (FL) at release (Fig. 2). Three modes were evident in 1991, but in 1992 the second mode centred at ~80 cm was missing in both species. The bigeye and yellowfin tagged in the Coral Sea were generally larger than

those tagged in other areas during the RTTP, where the size at release rarely exceeded 60 cm (Hampton 1992).

Recovery procedures

Fishers, processors, cannery workers and others in the industry were informed of the objectives and instructed how to return recovered tags. In Australia, all fishers involved in the east coast tuna fishery were provided with information through posters, articles in fisheries magazines and port visits. Those who found tagged fish were asked to send the tag number, catch location, date, fishing method, fish length and weight to SPC or CSIRO in return for a cap, T-shirt or \$A10.

Analytical methods

A tag-attrition model (Kleiber *et al.* 1987; Hampton *et al.* 1996) describes the rate of change in the return of tags over time. Changes occur because natural mortality, fishing mortality and emigration reduce the size of the tagged population over time, and because of changes in fishing effort. The model must also account for losses of tags through non-reporting and tag shedding. Consider a cohort of N_0 tagged fish released into a fishery at time t = 0. The two equations used to predict the number of tag returns $\hat{r_i}$ during time period *i* are

$$\hat{r}_i = \alpha N_i \frac{F_i}{F_i + X} \left[1 - \exp(-F_i - X) \right]$$
 (1)

and

$$N_{i+1} = N_i \exp(-F_i - X) \tag{2}$$

where α is the proportion of tags remaining viable after losses such as immediate tag shedding and non-reporting of recovered tags, N_i is the number of tagged tuna alive at the beginning of period *i*, F_i is the fishing mortality rate in period *i*, and X is the sum of the instantaneous rates of natural mortality, permanent emigration from the area under consideration and possibly other continuous tag losses (assumed constant over time), hereafter referred to as the attrition rate.

The tagged populations to be modelled are those remaining available to the Cairns-based longline fleet. Therefore, the model was applied to returns of tagged bigeye and yellowfin from this fleet, aggregated by quarterly time periods (February–April, May–July, August–October and November–January). Returns by fleets outside the area of operation of the Cairns-based longline fleet are disregarded, and can be viewed as being incorporated into the parameter *X*.

We had to assume values for α , because this parameter cannot be estimated accurately from tag-return data. The main processes likely to affect α

Table 1.Tag releases and returns of bigeye and yellowfin tuna, by fleet, tagged in the north-western
Coral Sea in 1991 and 1992

	Bigeye	tuna	Yellowfin tuna		
	1991 releases	1992 releases	1991 releases	1992 releases	
No. releases	3716	561	2511	394	
Returns by					
Tagging vessel	45	1	4	0	
Coral Sea handliners	10	0	4	0	
(Australian and Japanese ves	sels)				
Australian longliners	144	17	28	4	
Western Pacific longliners	32	4	14	2	
Western Pacific purse-seiners	5	1	22	3	
Western Pacific pole-and-liners	1	0	1	0	
Total returns	237 (6.4%)	23 (4.1%)	73 (2.9%)	9 (2.3%)	



Fig. 2. Size distributions of bigeye and yellowfin tuna releases in the north-western Coral Sea in 1991 and 1992. The lower dark histograms in each case indicate the release sizes of recaptured tagged tuna.

are tag shedding and non-reporting of recovered tags. For the RTTP as a whole, tag-shedding rates appear to be low: ~10% of tags are shed after 2 years (Hampton 1997). The mean reporting rate for the RTTP has been estimated to be ~0.6, although this estimate applies mainly to returns by purse-seiners (Hampton 1997). As longliners handle each fish separately, the reporting rate is probably higher. Thus, for the model fits, we chose a wide range of α (0.5–1.0) that should encompass its true value.

The parameters of the model specified by Eqns (1) and (2) are X and F_{i} . In practice, we cannot independently estimate *i* fishing mortality rates. However, fishing effort data, f_i , can be used to re-parameterize F_i as $F_i = qf_i$, where q is the catchability coefficient. For the Coral Sea data, there is strong evidence that q varies seasonally. We therefore used four catchability coefficients for the four 3-month quarters, i.e.

$$F_{y,s} = q_s f_{y,s} \tag{3}$$

where the subscripts *y* and *s* denote the year and quarter, respectively. We therefore estimate five parameters for each fit, *X* and q_s (*s* = 1, 2, 3 and 4).

Parameters are estimated by maximum likelihood using a multinomial likelihood function. This involves maximizing the likelihood, ℓ , of the observed data, **r**, given the model predictions $\hat{\mathbf{r}}$, i.e. maximize

$$\ell(\mathbf{r}|\hat{\mathbf{r}}) = \frac{N_0!}{(\Pi_i r_i!)(N_0 - \Sigma_i r_i)!} \left(1 - \frac{\Sigma_i \hat{r}_i}{N_0}\right)^{(N_0 - \Sigma_i r_i)} \prod_i \left(\frac{\hat{r}_i}{N_0}\right)^{r_i}$$
(4)

We used a quasi-Newton method to minimize the negative log of Eqn (4) and so derive maximum-likelihood estimates of X and q_s . A parametric bootstrap (Efron 1982) with 1000 replicates was used to estimate coefficients of variation for the parameters and their correlation matrix.

Results

Tag returns

By 30 March 1997, 361 recaptures from the 1991 releases and 35 recaptures from the 1992 releases had been reported (Table 1). The return rate for both species is marginally higher for the 1991 releases. Tag returns were generally scattered across the range of release lengths, although no returns had yet been received from the smaller mode of the 1992 yellowfin releases (Fig. 2). Tagged bigeye and yellowfin were recaptured in the release area by the tagging vessel, by Australian longliners and by Australian and Japanese longliners using handlines to catch bigeye and yellowfin from aggregations. Smaller numbers of returns were received from Japanese and New Caledonian longliners fishing in the surrounding Coral Sea and from longline, pole-and-line and purse-seine fleets fishing in the Solomon Islands, Fiji, Papua New Guinea and Micronesia (Table 1). Tagged yellowfin appeared to be more vulnerable than tagged bigeye to capture by purse-seiners; this is consistent with the overall results of the RTTP (Anon. 1995).

Temporal patterns of returns from the 1991 tag releases

Bigeye. Of the bigeye from the 1991 releases, 45 were recaptured within two weeks by the tagging vessel and an Australian longliner using handlines (Fig. 3*a*). Over the next



Fig. 3. Number of *(a)* bigeye and *(b)* yellowfin tuna tag returns from the 1991 releases, by month, for different fleets in the tropical western Pacific Ocean. The category 'Coral Sea handline' includes recaptures by the tagging vessel.

seven months, several tagged bigeye were recaptured by purse-seiners fishing in Solomon Islands and Papua New Guinea waters. Until May 1992, only one bigeye recapture was recorded by Australian longliners operating in the tagrelease area. Thereafter, recaptures by these vessels increased to August 1992, and were also reported by other longline fleets in the western Pacific. Few bigeye recaptures were recorded by Australian vessels longlining in the release area between September 1992 and April 1993. However, 10 tagged bigeye were recaptured in October–November 1992 on handlines used by Australian and Japanese longliners and by the tagging vessel during the 1992 release campaign. After November 1992, recaptures were almost exclusively by longliners fishing in the Coral Sea and the greater western Pacific.

The pattern of recaptures by the Australian longliners during 1993 and 1994 was similar to 1992: most recaptures were from May–August 1993 and April–September 1994. In 1995 and 1996, recaptures were also highest from May–August, but with some recaptures later in the year. Therefore, it appears that the bigeye forming the aggregations in October–November 1991 were strongly represented in the local bigeye population vulnerable to the Cairns-based longliners in the middle of the next five years.

Yellowfin. Soon after release, eight yellowfin were recaptured by handlining on the aggregations (Fig. 3*b*). Like bigeye, tagged yellowfin were being recaptured in the western Pacific purse-seine fishery (mostly near the Solomon Islands and Papua New Guinea) by early 1992. Unlike bigeye, yellowfin continued to be recaptured by these surface fleets through late 1993, though in small numbers. The pattern of yellowfin recoveries in the release area by Australian longliners is similar to that for bigeye. Few yellowfin were recaptured by these vessels before April 1992, but 11 were recaptured between April and August 1992. Only one recapture was reported between September 1992 and April 1993, after which recaptures were few and sporadic.

Temporal patterns of returns from the 1992 tag releases

Few tags from the 1992 releases were returned: 23 bigeye and 9 yellowfin. Most of these fish were also recaptured between April and August.

Tag-attrition model

The tag-attrition model was fitted to bigeye and yellowfin tuna tag returns from the Cairns-based longline fleet. Only returns from the 1991 releases are used in this analysis. Initially, we used the observed longline effort as reported in logbooks as estimates of $f_{y.s.}$. The tag-release, tag-return and longline-effort data used in the analysis are given in Table 2.

There is a strong and consistent periodicity in the estimated catchability coefficients for bigeye: they peak in May– July and fall by about a factor of ten in February–April (Table 3). A model with a single, non-seasonal catchability coefficient resulted in a highly significant (P<0.001) degradation in Table 2. Data used in fitting the tag-attrition modelsBigeye effort is obtained by multiplying quarterly effort values by 0.17 (for
quarters occurring mainly in calendar year 1991), 0.15 (1992), 0.32 (1993),
0.86 (1994), 0.81 (1995) and 1.00 (1996). Yellowfin effort is obtained by
multiplying quarterly effort values by 0.75 (1991), 1.00 (1992), 0.65 (1993),
0.58 (1994), 0.35 (1995) and 0.50 (1996). Total tag releases, excluding recap-
tures made by the tagging vessel soon after release: bigeye, 3669 releases;
yellowfin, 2507

Mid of q	month uarter	Bigeye returns	Yellowfin returns	Effort (thousand hooks)	Bigeye effort (thousand hooks)	Yellowfin effort (thousand hooks)
1991	Dec	1	2	38	7	29
1992	Mar	0	1	47	7	47
	June	8	8	46	7	46
	Sept	3	2	34	5	34
	Dec	1	1	34	5	34
1993	Mar	2	0	45	15	30
	June	16	3	62	20	41
	Sept	2	0	67	21	44
	Dec	0	3	90	29	59
1994	Mar	5	1	123	106	72
	June	22	2	144	124	84
	Sept	13	0	132	114	77
	Dec	2	1	101	87	58
1995	Mar	0	0	189	153	66
	June	30	0	221	179	77
	Sept	13	2	188	152	66
	Dec	6	1	139	113	49
1996	Mar	1	0	217	217	108
	June	14	0	256	256	128
	Sept	0	0	167	167	84
	Dec	5	1	120	120	60

Table 3. Estimates of parameters of the bigeye tag-attrition model for different levels of α , and the coefficients of variation (CV) and correlation matrix for $\alpha = 1.0$. The effectiveness of the observed effort in targeting bigeye is assumed to be constant among years

Catchability coefficients (q: values shown have been multiplied by 10^5 to aid comparison) are subscripted by quarter: 1, Feb.–Apr.; 2, May–July; 3, Aug.–Oct.; 4, Nov.–Jan.

α	$X(\text{year}^{-1})$	q_1	q_2	q_3	q_4
0.5	0.22	1.42	14.70	6.51	3.26
0.6	0.22	1.19	12.30	5.44	2.73
0.7	0.23	1.03	10.57	4.68	2.34
0.8	0.23	0.90	9.27	4.10	2.05
0.9	0.23	0.80	8.26	3.65	1.83
1.0	0.23	0.72	7.44	3.29	1.65
CV	0.27	0.41	0.22	0.27	0.30
q_1	0.48				
q_2	0.86	0.42			
q_3	0.72	0.34	0.63		
q_4	0.55	0.27	0.47	0.39	

fit. The absolute values of the catchability coefficients are negatively correlated with the assumed values of α , but the seasonal pattern is consistent across the range of α . The estimated attrition rate of 0.22–0.23 year⁻¹, which incorporates true natural mortality and permanent movement away from the area of the Cairns-based longline fishery, is robust to changes in α over the range investigated. Observed and predicted tag returns show a high degree of correspondence (Fig. 4*a*). The coefficients of variation (CV) for the estimated parameters range from 0.22 to 0.41. The parameters show various degrees of positive correlation, with the highest correlation coefficients obtained for *X*–*q*₂ and *X*–*q*₃ (Table 3).

Similar, though somewhat weaker (significant at P<0.001), seasonal catchability is evident for the yellowfin fit (Table 4). The attrition rate in this instance is much higher (0.85–0.87 year⁻¹), which implies that yellowfin have higher natural mortality than bigeye, a stronger tendency to move out of the

study area into the greater WTP, or both. This fit, as indicated by the plot of observed and predicted tag returns (Fig. 4b) and by the CVs of the parameters (Table 4), is less impressive than the bigeye fit.

The relatively low attrition rate for bigeye and relatively high attrition rate for yellowfin might be an artifact of the assumption that the effectiveness of Cairns-based longline effort in catching bigeye and yellowfin did not change during the study. The time series of bigeye catch-per-unit-effort (CPUE) for Cairns-based longliners shows a seasonal pattern similar to the tag returns, coupled with an increasing trend (Fig. 5*a*). Conversely, the time series of yellowfin CPUE has a less consistent seasonal pattern and shows a declining trend. CPUE is affected by both abundance and catchability; the two effects cannot be distinguished with the present data. However, changes in the species composition of the catch over the period of the study (Fig. 5*b*) suggest that Cairns-based longliners have been targeting bigeye more in



Fig. 4. Observed and predicted (a) bigeye and (b) yellowfin tuna tag returns: model 1, constant-efficiency model; model 2, variable-efficiency model.

Table 4. Estimates of parameters of the yellowfin tag-attrition model for different levels of α , and the coefficients of variation (CV) and correlation matrix for $\alpha = 1.0$. The effectiveness of the observed effort in targeting yellowfin is assumed to be constant among years

Catchability coefficients (q: values shown have been multiplied by 10⁵ to aid comparison) are subscripted by quarter: 1, Feb.–Apr.; 2, May–July; 3, Aug.–Oct.; 4, Nov.–Jan.

α	$X(\text{year}^{-1})$	ear ⁻¹) q_1		q_3	q_4	
0.5	0.85	2.17	16.08	6.95	8.88	
0.6	0.86	1.81	13.42	5.81	7.42	
0.7	0.86	1.56	11.51	5.00	6.37	
0.8	0.87	1.37	10.08	4.38	5.58	
0.9	0.87	1.22	8.97	3.90	4.97	
1.0	0.87	1.10	8.07	3.52	4.48	
CV	0.17	0.74	0.41	0.61	0.39	
$\overline{q_1}$	0.21					
q_2	0.72	0.16				
q_3	0.54	0.12	0.41			
q_4	0.41	0.10	0.28	0.25		

recent years (by setting the longline deeper or setting at night), so some increase in efficiency with respect to bigeye is likely to have occurred. At the same time, a decrease in efficiency with respect to yellowfin, which tend to be found at shallower depths than bigeye, might be expected.

Let us assume that the trends in CPUE are entirely due to such changes in efficiency through improved bigeye targeting (and that the abundance of both species in the study area has been stable for the period of the study). We can then use the annual CPUEs for 1991 through 1996 (normalized to the maximum) to adjust the observed effort to 'bigeye-targeted' and 'yellowfin-targeted' effort series. The normalized CPUEs for bigeye for each year are 0.17, 0.15, 0.32, 0.86, 0.81 and 1.00, and for yellowfin 0.75, 1.00, 0.65, 0.58, 0.35 and 0.50. The observed, 'bigeye-targeted' and 'yellowfin-targeted' effort time series are shown in Fig. 6.

When the model is fitted to the bigeye data using the 'bigeye-targeted' effort, the attrition rate (0.52–0.59 year⁻¹) and the catchability coefficients are higher (Table 5) than when the observed effort is used. This model also provides a good fit to the data (Model 2 in Fig. 4*a*), and is marginally superior to the constant-efficiency model as indicated by the negative log-likelihood values (979.68 for the constant-efficiency model and 977.75 for the variable-efficiency model at $\alpha = 1.0$).

The yellowfin fit using the 'yellowfin-targeted' effort results in lower estimates of attrition rate (0.62–0.63 year⁻¹) than when the observed effort data are used (Table 6). The catchability coefficients are essentially unaffected. As for bigeye, the fit of the model to the yellowfin data (Model 2 in Fig. 4*b*) is slightly better than for the constant-efficiency model (negative log-likelihoods of 217.70 for the constantefficiency model and 216.95 for the variable-efficiency model at α = 1.0).

Movements of tagged tuna out of the release area

While most tag recaptures of both species were in the release area, some were in the adjacent Coral Sea and further afield to the north, east and south. Bigeye returns (Fig. 7*a*) came mainly from longliners in the Coral Sea in the area bound by Papua New Guinea, Solomon Islands, Vanuatu and New Caledonia. However, several bigeye were recaptured in the central Pacific, and some in Micronesia. The eastward extent of bigeye recaptures is $130^{\circ}-140^{\circ}$ W, the main Pacific bigeye fishing ground for Japanese longliners.

Tagged yellowfin were recaptured in considerable numbers throughout the Coral Sea and beyond (Fig. 7*b*). Most were caught by purse seiners, including two recaptures from equatorial waters east of 170°W after 19 months and 35 months at liberty. Two tagged yellowfin were recaptured in Japanese coastal waters by a purse seiner and a longliner, both after 31 months at liberty. These four recaptures are the longest yellowfin displacements (~3000 n.miles) recorded in the RTTP database. Several yellowfin were recaptured by Japanese longliners off the coast of southern Queensland and NSW, indicating some links with yellowfin taken in the east coast longline fishery in these areas.

Movements of tagged tuna from the WTP into the eastern AFZ

Only one recovery in the eastern AFZ of a tuna tagged during the RTTP outside Australian waters has been confirmed. The recovery — a yellowfin that had been tagged off the south coast of New Britain in Papua New Guinea — was made by an Australian longliner off the coast of Sydney, NSW. The tagged fish was at liberty for 32 months. Several other RTTP yellowfin tags have been recovered in Australian tuna canneries, but it is unlikely that the fish were caught in Australian waters.

Discussion

Bigeye and yellowfin exploitation by Cairns-based longliners

The tag returns by Cairns-based longliners, in combination with their catch-and-effort data, have provided useful information on some aspects of the bigeye and yellowfin stocks and their exploitation in this area. The highly seasonal tag returns and the CPUE for bigeye tuna, and to a lesser extent yellowfin tuna, are suggestive of seasonally variable catchability. Two hypotheses could be posed to explain such a pattern.

The first hypothesis is that changes in apparent catchability are mediated by seasonal movement of tuna into and out of the area. Yellowfin and bigeye would move into the northwestern Coral Sea in mid year and be caught by longlining. During the October–March spawning season (McPherson 1991), their aggregation and other behaviour associated with spawning would enable capture by handlining. After spawning, the tuna would disperse into the adjacent Coral Sea, and perhaps beyond, returning to the area in the middle of the next year. If this hypothesis is correct, we would expect tags



Fig. 5. (a) Quarterly bigeye and yellowfin tuna catch-per-unit-effort and (b) ratio of bigeye to yellowfin tuna catch, by Cairns-based longliners in the area $14^{\circ}-20^{\circ}$ S, $145^{\circ}-153^{\circ}$ E during the study period.

to be returned from the adjacent Coral Sea and WTP mainly in the first half of the year. In fact, these tags have been returned in the same seasons as those in the study area (Fig. 8), which does not support this seasonal-movement hypothesis.

The second hypothesis is that bigeye and yellowfin gradually disperse from the release area, but that large numbers of bigeye (in particular) remain resident in the area for some time. Seasonal variation in environmental parameters that influence the vertical distribution of the tuna (or seasonal changes in tuna behaviour) would result in the variations in catchability reflected in the tagging and CPUE data. Evaluation of this hypothesis requires some consideration of bigeye and yellowfin behaviour in relation to environmental variables, particularly temperature and dissolved oxygen, which are believed to be the key determinants of vertical distribution of tuna (Brill 1994).

During the day, bigeye are thought to prefer ambient water temperatures in the range 11–17°C (Hanamoto 1987; Holland *et al.* 1990; Boggs 1993), from which they make periodic, brief excursions into warmer water at the interface of the thermocline and upper mixed layer (Holland *et al.* 1990). These upward excursions are believed to be for thermoregulation (Holland *et al.* 1990, 1992; Holland and Sibert 1994). At night, bigeye tend to rise to the upper mixed layer, presumably feeding on prey that also move vertically at night (Holland *et al.* 1990). In contrast, yellowfin tend to inhabit



Fig. 6. Time series of observed effort, 'bigeye-targeted' effort and 'yellowfin-targeted' effort by Cairns-based longliners during the period of the study.

Table 5. Estimates of parameters of the bigeye tag-attrition model for different levels of α , and the coefficients of variation (CV) and correlation matrix for $\alpha = 1.0$. The effectiveness of the observed effort in targeting bigeye is assumed to be proportional to the observed commercial catch-per-unit-effort in the different calendar years

Catchability coefficients (q: values shown have been multiplied by 10⁵ to aid comparison) are subscripted by quarter: 1, Feb.–Apr.; 2, May–July; 3, Aug.–Oct.; 4, Nov.–Jan.

 $X(\text{year}^{-1})$ α q_1 q_2 q_3 q_4 0.52 5.49 0.5 62.58 30.37 17.61 0.6 0.54 4.75 54.07 26.18 15.13 0.7 0.56 4.18 47.61 23.01 13.27 0.57 11.81 0.8 3.74 42.54 20.53 0.9 0.58 38.44 18.53 10.65 3.38 1.0 0.59 3.09 35.07 16.89 9.69 CV 0.14 0.37 0.21 0.28 0.43 0.32 q_1 0.79 0.33 q_2 0.70 0.31 0.53 q_3 0.41 0.02 0.40 0.35 q_4

the mixed layer and the upper 1-2 °C of the thermocline, moving to shallower depths during the night.

Logbook data indicate that Cairns-based longliners typically begin setting their gear in the late morning to early afternoon (Fig. 9). As many as 1500 hooks have been set in a fishing operation, but most have 400–700 hooks. Soak time is highly variable (1–20 h, mean 8.5 h), but the typical set fishes mostly during the day. Therefore, hooks would need to fish in water <17°C to target bigeye tuna effectively. Table 6. Estimates of parameters of the yellowfin tag-attrition model for different levels of α , and the coefficients of variation (CV) and correlation matrix for $\alpha = 1.0$. The effectiveness of the observed effort in targeting yellowfin is assumed to be proportional to the observed com-

mercial catch-per-unit-effort in the different calendar years Catchability coefficients (q: values shown have been multiplied by 10^5 to aid comparison) are subscripted by quarter: 1, Feb.–Apr.; 2, May–July; 3, Aug.–Oct.; 4, Nov.–Jan.

α	$X(\text{year}^{-1})$	q_1	q_2	q_3	q_4	
0.5	0.62	2.16	15.07	6.23	9.03	
0.6	0.62	1.80	12.56	5.20	7.53	
0.7	0.62	1.54	10.77	4.46	6.46	
0.8	0.62	1.35	9.42	3.90	5.66	
0.9	0.62	1.20	8.37	3.47	5.03	
1.0	0.63	1.08	7.54	3.13	4.53	
CV	0.29	0.85	0.38	0.61	0.50	
q_1	0.19					
q_2	0.62	0.11				
q_3	0.39	0.06	0.25			
q_4	0.42	0.03	0.46	0.06		

Thermal profile data from the World Ocean Atlas (WOA) (Levitus and Boyer 1994*a*) for the area 15–20°S,145–150°E show that the 17°C isotherm is found at about 280 m, and that the mixed layer is weakly defined during summer but more pronounced (<100 m in depth) in mid year (Fig. 10). Recent data from archival tags attached to the branch (fishing) lines of Cairns-based longliners (CSIRO, unpublished) suggest that the lines rarely fish at depths >200 m. If these data are representative of longline sets made by Cairns-based long-



Fig. 7. Displacements of *(a)* bigeye and *(b)* yellowfin tuna tagged in the north-western Coral Sea in 1991 and 1992. Arrowheads: recaptures by long-liners. Stars: recaptures by purse seine or pole-and-line vessels.

liners, and if the vertical distribution of bigeye in this area is consistent with published data from other areas, day sets would be likely to capture bigeye only during the periodic excursions of the tuna to the top of the thermocline. On the other hand, yellowfin, which stay in the upper mixed layer during both the day and the night, would be more vulnerable to capture by Cairns-based longliners, and this would explain their much higher CPUE.

The WOA data do not indicate a seasonal upward shift of 11–17°C water that could explain the higher mid-year bigeye CPUE and tag recaptures. Neither does dissolved oxygen



Fig. 8. (\blacksquare) Bigeye and (\Box) yellowfin returns, from releases in the north-western Coral Sea in 1991 and 1992, by vessels fishing in the adjacent Coral Sea and WTP, aggregated by month.

appear to limit the vertical habitat of bigeye or yellowfin in this region. Minimum dissolved oxygen tolerances for bigeye of around 2.3 mL L⁻¹ (Bushnell *et al.* 1990) and for yellowfin of around 3.3 mL L⁻¹ (Brill 1994) have been proposed; WOA data (Levitus and Boyer 1994*b*) indicate that dissolved oxygen is above these limits to at least 1000 m depth in the north-western Coral Sea.

What then could induce the consistent seasonal patterns observed in the bigeye tag returns and CPUE? One possibility is that there are seasonal small-scale upwellings of cooler water that are not apparent in the WOA temperature data, and that Cairns-based longliners are targeting these areas to increase their bigeye catch. Another possibility is that there is a seasonal change in behaviour - perhaps associated with the formation of spawning aggregations — that brings bigeye into warmer, more highly oxygenated water closer to the surface, and hence within range of the longline gear. A third possibility is that the more distinct interface between the thermocline and mixed layer during the mid-year period provides a more consistent focal point for bigeye during daytime upward excursions, which makes them more vulnerable to longlining; Holland et al. (1990) found that bigeye consistently terminated their upward excursions at the bottom of the mixed layer, rather than at any absolute ambient temperature. Finer-scale oceanographic data and data on the vertical movements of bigeye tuna (from archival or sonic tags) in the north-western Coral Sea would be required to resolve these questions.

If the observations on bigeye vertical movements (Holland *et al.* 1990) are valid for the north-western Coral Sea, we would expect longline sets that fished during the night to achieve better bigeye catches than day sets. Since late 1994, longline sets have more often been started in the late afternoon and early evening (Fig. 9), which might explain the concurrent increase in bigeye CPUE and weakening of the seasonal signal (Fig. 5a).



Fig. 9. Distribution of start of set times by Cairns-based longliners, by quarter.



Fig. 10. Average temperature–depth curves in the area 15° –20°S, 145° –150°E for January, April, July and October (data from Levitus and Boyer 1994*a*).

Fishing mortality, exploitation and attrition rates

Average local fishing mortality rates can be computed from the estimated catchability coefficients and effort data. For both species, fishing mortality increased over the duration of the study. For bigeye, the estimated 1996 local fishing mortality rate reached 0.028–0.056 year⁻¹. (for $\alpha = 1.0$ –0.5) for the constant-efficiency hypothesis, and 0.137–0.244 year⁻¹ for the variable-efficiency hypothesis. These represent exploitation rates (ratio of fishing mortality rate to attrition rate plus fishing mortality rate) of up to 0.20 and 0.32, respectively. For yellowfin, the corresponding 1996 fishing mortality estimates are 0.035–0.068 year⁻¹ for the constantefficiency hypothesis, and 0.016–0.032 year⁻¹ for the variable-efficiency hypothesis, representing exploitation rates of up to 0.07 and 0.05, respectively.

The estimated attrition rates comprise natural mortality, permanent movement away from the area fished by Cairnsbased longliners and possibly other minor sources of continuous tag loss. The attrition rates for yellowfin estimated with high assumed reporting rate under the constant-efficiency (0.87 year⁻¹) and variable-efficiency (0.63 year⁻¹) assumptions are reasonably consistent with previous estimates of natural mortality for yellowfin (Cole 1980; Suzuki 1994; Wild 1994). The attrition rate for bigeye estimated under the constant-efficiency assumption (0.23 year⁻¹) is considerably lower than the natural-mortality estimate of 0.36 year⁻¹ by Suda and Kume (1967). Given that our estimate contains a movement component, the natural-mortality component would be somewhat less than the attrition-rate estimate. The attrition-rate estimate under the variable-efficiency assumption (about 0.59 year⁻¹) is more consistent with the previous estimate of natural mortality. However, given that the bigeye tag releases consisted of mainly medium- to larger-sized (60–100 cm) fish, the possibility of a natural-mortality rate consistent with the smaller attrition-rate estimate should not be discounted.

Relationship of stocks in the north-western Coral Sea to those in the WTP

The capture of substantial numbers of tagged bigeye and yellowfin tuna in the adjacent Coral Sea and WTP clearly indicates that the fish exploited by Cairns-based longliners mix to some extent with tuna stocks in the western Pacific region. The absence, to date, of recaptures by Cairns-based longliners of tuna released elsewhere in the WTP leaves open the question of the origin(s) of tuna in the north-western Coral Sea. The absence of such recaptures is consistent with the hypothesis that these fish originate mainly from local spawning. However, the relatively low tuna-fishing activity would make the probability of capturing tagged immigrants, if they were present, very small. Some light may be shed on this question through present research projects on the genetic structure of Pacific yellowfin and bigeye stocks and geographical variation in otolith micro-chemistry (Gunn and Ward 1994).

Relationship of stocks in the north-western Coral Sea to those in the south-eastern AFZ

Yellowfin spawning in the north-western Coral Sea could theoretically contribute to recruitment of yellowfin to the south-eastern AFZ longline fishery through larvae and juveniles being transported in the southward-flowing East Australian Current (Anon. 1989; McPherson 1991). Although we have no information on the geographical origin of tuna tagged in the north-western Coral Sea, there is evidence from the tagging data that some fish of both species move south from the tag-release area. It is also possible that tuna from the adjacent WTP may contribute to that component of the stock in the south-eastern AFZ, as indicated by the recapture off the south coast of New South Wales of a tagged yellowfin released in Papua New Guinea. The number of recaptures in the south-eastern AFZ is small, but it is significant given the relatively small catch in this area.

Management implications

Although many questions remain, the tagging study provides some useful information in the context of yellowfin and bigeye tuna management in the eastern AFZ.

If the rate of tag reporting and other sources of tag loss are within the range assumed in this paper, recent exploitation rates for yellowfin in the north-western Coral Sea appear to be low, and significant local depletion of the stock is not likely at existing levels of effort. Recent exploitation rates for bigeye are estimated to be higher (up to about 0.3), particularly if the hypothesis of increased bigeye targeting by Cairns-based longliners is correct, warranting a cautious approach to further expansion of the fishery.

The impact of targeting assumptions on the results of the bigeye analysis in particular demonstrates the need to understand how different fishing practices (such as time of set and fishing depth) affect the efficiency of effort, and to collect data on such fishing practices so that changes in efficiency can be accounted for in stock assessments.

Clear links between yellowfin and bigeye in the northwestern Coral Sea and those in the adjacent WTP and beyond have been demonstrated. Some link with the south-eastern AFZ is also likely. Such links can be expressed in population models with spatial structure (Sibert *et al.* 1996), enabling the possible effects of management decisions in one area upon other areas to be assessed.

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