CSIRO PUBLISHING

Marine and Freshwater Research, 2010, **61**, 1134–1146 www.publish.csiro.au/journals/mfr

Spatial and fishing effects on sampling gear biases in a tropical reef line fishery

David J. Welch[A,B,E], *Bruce D. Mapstone*[C], *Campbell R. Davies*[C] *and Garry R. Russ*[D]

[A]Queensland Primary Industries and Fisheries, Department of Employment, Economic Development and Innovation, PO Box 1085, Oonoonba, 4811 Qld, Australia.
[B]Fishing and Fisheries Research Centre, James Cook University, Townsville, Qld 4811, Australia.
[C]CSIRO Marine and Atmospheric Research, Castray Esplanade, Hobart, Tas. 7005, Australia.
[D]School of Marine and Tropical Biology and ARC Centre for Coral reef Studies, James Cook University, Townsville, Qld 4811, Australia.
[E]Corresponding author. Email: david.welch@jcu.edu.au

Abstract. Biased estimates of population parameters for harvested stocks can have severe implications for fishery management strategy choices. Hook-and-line fishing gear is size-selective and therefore collects biased samples from wild populations. Such biases may also vary in space and time. To assess this assertion, we compared line- and spear-caught samples of the main target species of an Australian hook-and-line fishery to quantify relative bias in size and age structure estimates. We also assessed the consistency of biases among four fishery regions and between two management zones – areas open and closed to fishing. Fish less than 310 mm and younger than 4 years comprised a larger proportion of the speared than the line samples regardless of region or management zone. Conversely, hook-and-line sampled more fish in larger size classes (>370 mm) and older age classes ($\geq$6 years) relative to spear fishing. These biases were qualitatively, but not quantitatively, consistent in all regions and management zones. This variation in sampling resulted in different inferences about regional and zone-related patterns in population size and age structure. We recommend careful consideration of sampling bias when drawing conclusions about regional and management zone effects on fish populations.

Additional keywords: bias, coral trout, Great Barrier Reef, hook-and-line, no-take zones, selectivity, spearfishing.

Introduction

Age and length data of fish are central inputs to most modern fisheries' assessment methods (Hilborn and Walters 1992; Quinn and Deriso 1999; Haddon 2001). Basic information about growth, mortality, and recruitment of fish populations is derived directly from size-at-age data. Length-based methods can be used to derive estimates of these parameters but there are many examples of large variation in size-at-age and poor definition of year-classes in length–frequency distributions, especially in tropical species (Bullock *et al.* 1992; Ferreira and Russ 1995; Williams *et al.* 2003). It follows that size frequencies often do not reflect age frequencies of a population and the resulting estimates of derived population parameters, such as those describing cohort strength, growth, and mortality, may be biased to varying degrees. Hence, length-based methods of parameter estimation (e.g. Petersen method, Pauly 1984) are relatively unreliable for species that display these life history characteristics, particularly longer-lived species with asymptotic maximum sizes reached relatively early in life (Morales-Nin and Ralston 1990; Morison *et al.* 1998). Age distributions are preferred over length distributions where possible in such circumstances. Reliable age distributions are also powerful tools for providing information about recruitment history from point samples of a population (Jones 1991; Russ *et al.* 1996; Horn 1997).

The size and age structures of fish populations also can identify differences in biological characteristics of populations from different locations that may indicate discrete stocks (Begg *et al.* 1999), different environmental or physical conditions, variation in recruitment history, or impacts of fishing on wild populations. Such regional differences may indicate variation in the productivity of stocks or the impacts of fishing and signal a need for different harvest management strategies in different regions (Begg *et al.* 2005; Mapstone *et al.* 2008).

Two assumptions central to using size and age data in monitoring fish populations are that: (i) samples are as representative as possible of the population from which they came; and (ii) sampling biases are relatively consistent over space and time (Hilborn and Walters 1992). The first is difficult to achieve primarily due to the size-selective nature of fish sampling gears (Hovgard and Riget 1992). For example, the size frequency of a

 10.1071/MF09278 1323-1650/10/101134

sample taken by hook-and-line gear may be influenced by the size and gape of the mouth of a species relative to hook size and by the size of the bait (Cortez-Zaragoza *et al.* 1989; Karpouzi and Stergiou 2003; Alós *et al.* 2008). Samples collected using gill-nets will depend on fish girth relative to the mesh size (Hamley 1975; Hilborn and Walters 1992), while trawl samples are influenced by the avoidance capabilities of individuals, typically meaning that larger fish are less likely to be retained by the gear due to their higher swimming speeds and capacity to avoid or escape the gear. Other factors that influence the size structure of fish catches are more difficult to quantify. These include size-specific behaviours such as competition for baits (e.g. Bertrand 1988; Lokkeborg and Bjordal 1992) and size-dependent variation in the distribution of fish (Morales-Nin and Ralston 1990; Hilborn and Walters 1992). Competition for baits and other behaviour-related effects also might be density-dependent and modified by the effects of fishing on population structure, so effective selectivity might vary spatially or temporally with effects of fishing.

Comparison of samples from different times, places or populations is predicated on the assumption that sampling biases are relatively constant. Change in sampling bias in space and time would clearly confound comparisons of populations in different places and times. Sampling bias may be influenced by factors such as habitat structure, sampling depth, and size-dependent spatial or temporal variation in abundance. Sampling bias also may be affected by population density. For example, exposure or access to the sampling gear may be influenced by social feeding hierarchies or where a species is cannibalistic (St John *et al.* 2001). Thus, impacts of fishing on population structure or density may also influence sampling bias.

We sampled populations of the common coral trout, *Plectropomus leopardus* (Serranidae : Epinephelinae), as part of a large-scale adaptive management experiment on the Great Barrier Reef (GBR), the Effects of Line Fishing (ELF) Experiment (Mapstone *et al.* 1996*a*; Campbell *et al.* 2001; Mapstone *et al.* 2004, 2008). *P. leopardus* is the major target of the multispecies Reef Line Fishery on the GBR and fetches a high premium on Asian markets as a live product (Welch *et al.* 2008). A primary objective of the ELF experiment was to provide estimates of important population parameters to parameterise a spatially explicit management strategy evaluation model (ELFSim) to evaluate the relative performance of fisheries and conservation management strategies for the GBR (Little *et al.* 2007; Mapstone *et al.* 2008). The aim of this study was to provide the empirical basis for estimating bias associated with hook-and-line fishing, the primary monitoring method used for the fishery, by examining the size and age structures of *P. leopardus* sampled by spear fishing and hook-and-line. We hypothesised that hook-and-line gear would: (i) under-sample smaller and younger fish compared with spearfishing (because of gape limitations on small fish taking large baits); and (ii) sample a greater proportion of fish in the larger size and age classes than spear fishing. Our key focus, however, was to test the null hypotheses that such biases would be unaffected by either region, management zone, or their interaction. These regions and zones were expected to be subject to different fishing histories and have different population densities of *P. leopardus* (Mapstone *et al.* 2004).

Methods

Data collection

Data collection was part of the ELF Experiment, which involved sampling at four clusters, each of six reefs spread over 7° of latitude along the GBR. Two reefs in each cluster were zoned ‘open to fishing’ (‘fished’) and four had been zoned ‘closed to fishing’ (‘no-take’) for 10–12 years when the ELF Experiment began (1995). All reefs were sampled by hook-and-line for which methods are fully described in detail by Mapstone *et al.* (2004) and Davies *et al.* (2006). Two of the no-take reefs and the two fished reefs were also sampled by spear fishing in 1995 for this study. The clusters were assumed to capture regional variation in fishing and population structure of coral trout. The clusters were in the Lizard Island (~14°52S, 145°30E), Townsville (~18°30S, 147°35E), Mackay (~20°25S, 150°10E), and Storm Cay (~21°20S, 151°20E) regions, from north to south, respectively.

Spear fishing surveys

All spear fishing was done on SCUBA during one field trip to each region within 1 week after the hook-and-line surveys. Sampling was structured similarly to the hook-and-line surveys except that sampling was restricted to a maximum depth of 10 m to satisfy safety requirements of repetitive diving. The hook-and-line data used in this study were of both depth strata combined as this represented the full potential of hook-and-line sampling. Spear sampling effort was spread evenly among and within the six blocks in two ways: (i) using two depth strata, shallow (0–5 m depth) and deep (5–10 m depth); and (ii) with two sampling teams of two divers diving different locations within each block. One fisher in each team sampled the shallow stratum and the other the deep stratum in each dive, giving a total of 24 person-dives per reef (six blocks*two depths*two sampling teams). Search times (bottom times) were set at 30 min per dive except where high catch rates resulted in prematurely reaching permitted catch limits per reef.

Spearing procedure

A block was randomly selected and divers haphazardly selected a point of entry and swim direction in reef slope areas that allowed sampling to a depth of 10 m. Divers used SCUBA to minimise the potential for bias towards sampling large fish over small fish during searching as smaller fish were more difficult to locate visually and were likely to be overlooked during free-dive spear fishing. Horizontal search horizon was limited to an estimated 6 m, which was within the expected limits of underwater visibility and allowed for the fact that larger fish are easier to sight over larger distances, further minimising potential size-related sampling bias. The fisher attempted to capture fish during each dive according to a strict target selection protocol developed in an earlier pilot study (D. Welch, unpubl. data), as follows. The fisher attempted to spear every lone fish seen, irrespective of size. When groups of fish (multiple encounter) were seen, the fisher targeted the first fish seen. At the second multiple encounter the second fish sighted in the group was targeted and so on up to a maximum of five fish per group. After going through the sequence of fish 1–5, the number of the fish to be speared started again at the first fish seen in a multiple encounter. If the fisher was due to spear the fourth fish sighted in a multiple encounter of three fish, then the third sighted would be speared (i.e. the one closest to the fourth).

All spear fishers used the same equipment and method of capture. Captured fish were immediately threaded on to a stainless steel wire attached to a surface float small enough to be dragged to the bottom by the fisher to attach fish as required, so avoiding repeated ascents and descents during each dive. All fish were measured for length (fork length, mm) in the boat at the completion of each dive. Each fish had a coded tag attached and was frozen for later analysis.

Age determination

Speared samples

Otoliths of *P. leopardus* show a pattern of translucent and opaque zones that have been identified as annual increments (Ferreira and Russ 1994). Otoliths from speared samples were generally immersed in 'baby oil' (Johnson & Johnson, New Brunswick, NJ, USA) and read whole under a dissecting microscope at 40× magnification and illuminated by reflected light against a black background. Smaller otoliths were read under lower magnification (20×) with reduced light, as this greatly enhanced identification of annuli. Information about the position of the margin relative to the last complete increment, and the readability of each otolith also was recorded. The margin was classified as opaque, <50% translucent or >50% translucent, based on the width of the last complete increment. The otolith was given a readability index from 1 (very clear) to 3 (very poor).

Ferreira and Russ (1994) reported that whole readings of sagittae for *P. leopardus* underestimate age compared with readings of sectioned otoliths at ages above 6 years, with underestimation of age increasing with age. Accordingly, all whole otoliths with a count of six annuli or more were subsequently sectioned and re-read. Any other whole otoliths that had a readability index of 3 were also sectioned. The methods used for processing sectioned otoliths are described by Davies *et al.* (2006). Sectioned otoliths were read in random order, recording the same information as for whole otoliths. Annuli were counted on the distal surface in the posterior dorsal region of each sagitta. The age estimates from sections then replaced those from the corresponding whole otoliths. The right sagitta was used whenever possible for consistency in age determination.

Precision of age estimates

Ten otoliths were selected at random from each age class 1 to 10 years to estimate the precision, or repeatability, of counts of otolith increments. All otoliths with counts greater than 10 years were pooled into an 11th (11+) age class. This subsample of otoliths ($n = 124$) were then re-sorted in random order and read a second and third time. The repeat readings of the otoliths were spread over three reading occasions, with a minimum of 2 weeks between each reading, and otoliths rerandomised between occasions to minimise the potential for prior knowledge of individual otoliths to cause bias in age estimation. The coefficient of variation (CV; Chang 1982) was then calculated for each otolith as the standard deviation of repeated counts divided by their mean and averaged over all age classes to give a value for the entire sample. The CV was a satisfactory comparative indicator of precision in this case because the sample sizes were equal for all groups.

Hook-and-line samples

Final ages for sagittal otoliths taken by hook-and-line were derived also following Ferreira and Russ (1994); however, all otoliths were sectioned as per Davies *et al.* (2006) and multiple readers used to read all otoliths two or three times with acceptance of a final age requiring agreement between at least two of the multiple readings (Mapstone *et al.* 2004; Lou *et al.* 200). A random sample of otoliths ($n = 44$, age range 1–13 years) was taken from the speared sample and read three times by one of the main readers used to age fish from the line-caught samples (Ashley Williams – AW) and also the reader of the speared sample (DW) to test reader consistency in age estimates between samples. The percentage agreement between readers was calculated and the CV was calculated for each reader and compared. Percentage agreement was the number of age estimates agreed within a specified number of years between readers and expressed as a percentage of the total number of age estimates (Kennedy 1970).

The CV for the speared samples read multiple times, pooled across all age classes, was 0.081. CV for different readers of otoliths were similar at 0.060 (DW) and 0.050 (AW). Percentage agreement between DW and AW was 61.36% for exact agreement and 90.90% for agreement to within ±1 year. These values were considered an acceptable level of precision between readers (Chang 1982) and indicated that comparisons of age data from line- and spear-caught samples was unlikely to be confounded by reader-specific biases.

Data analysis

Mean size and age

Mean size and age were calculated for each reef from both gear samples and compared between methods (hook-and-line, spear) among regions, zones and reefs by four-way Analysis of Variance (ANOVA). The factors were method (spear, line), region (Lizard Island, Townsville, Mackay, Storm Cay), and management zone (fished, open to fishing; no-take, closed to fishing), all considered fixed effects, and reef as a random variable nested within region and zone. The primary interest in these analyses was in any interactions of Method with Region or Zone or both. It was expected that the methods would have different overall sampling biases but we were particularly interested in whether, and how, the effect of Method changed (difference in bias) among different regions or management zones, and whether such variation would result in different inferences about Region or Zone effects. *Post hoc* pairwise comparisons, where appropriate, were done using the Tukey–Kramer test for unequal sample sizes (Sokal and Rohlf 1981).

Population size and age structure

A four-way frequency analysis was used to develop a log-linear model for each of size and age structures taken by spear and hook-and-line in different regions and management zones, with samples pooled among reefs within each region and zone.

Log-linear models are sensitive to low expected cell values and it is recommended that all expected frequencies are greater than zero and no more than 20% of cells have expected frequencies less than five to maximise the power of the test and minimise the probability of spurious significant effects (Tabachnick and Fidell 2006). Size bins of 30 mm best achieved these criteria for the size data while still retaining reasonable numbers of bins to adequately describe the population size structure. Nine size bins were used for each method, ranging from 310–340 to 490–520 mm, with fish <310 and >520 mm pooled into the smallest and largest bins, respectively. A total of 144 cells were used over the four regions, two management zones, and two methods, with all expected frequencies >1 and only nine <5. Seven age classes were found to best satisfy the criteria for the age data. There were only four 1-year-old fish in the entire hook-and-line sample, so it was necessary to pool all fish ≤2 years. It also was necessary to pool fish 8 years and older (≥8 years). A total of 112 cells were used for age frequencies, with only nine cases having expected frequencies of <5.

The log-linear analysis was begun by fitting the following fully saturated model to the data:

$$\ln(f_{ijkl}) = \mu + \lambda_i^M + \lambda_j^R + \lambda_k^Z + \lambda_l^{S,A} + \lambda_{ij}^{MR} + \lambda_{ik}^{MZ} + \lambda_{il}^{MS,A} + \lambda_{jk}^{RZ} + \lambda_{jl}^{RS,A} + \lambda_{kl}^{ZS,A} + \lambda_{ijk}^{MRZ} + \lambda_{ijl}^{MRS,A} + \lambda_{ikl}^{MZS,A} + \lambda_{jkl}^{RZS,A} + \lambda_{ijkl}^{MRZS,A}$$

where f_{ijkl} = the frequency of individuals in size (or age) class l collected by method i from zone k in region j, μ = the average of the logs of the frequencies in all cells, λ_i^M = the effect of the ith Method (spear, hook-and-line), λ_j^R = the effect of the jth Region (Lizard Island, Townsville, Mackay, Storm Cay), λ_k^Z = the effect of the kth Zone (fished, no-take), $\lambda_l^{S,A}$ = the effect of the lth Size or Age class (described above), λ_{ij}^{MR}, λ_{ik}^{MZ}, $\lambda_{il}^{MS,A}$, λ_{jk}^{RZ}, $\lambda_{jl}^{RS,A}$, $\lambda_{kl}^{ZS,A}$ = the effects of the two-way interactions between factors, λ_{ijk}^{MRZ}, $\lambda_{ijl}^{MRS,A}$, $\lambda_{ikl}^{MZS,A}$, $\lambda_{jkl}^{RZS,A}$ = the effects of the three-way interactions among factors, and $\lambda_{ijkl}^{MRZS,A}$ = the effect of the four-way interaction among factors.

A step-down elimination process, beginning with the highest-order interaction, was then used to identify the most parsimonious model to explain the data, with $\alpha > 0.05$ set as the criterion for eliminating terms from the model. The relative impact of eliminating terms from the model at each step was assessed from the change in Likelihood-Ratio (L-R) Chi-square value from that for the previously fitted model. The Method*Size or Method*Age terms were of only limited interest in this study because a difference between methods was to be expected. The terms of primary interest were Method*Region*Size (or Age), Method*Zone*Size (or Age) and Method*Region*Zone*Size (or Age). *Post hoc* Chi-square tests were done to determine causes of significant interaction effects (Bakeman and Robinson 1994).

Results

A summary of samples collected by each method (hook-and-line, spear) in each region and management zone, and the corresponding size and age data, are presented in Table 1.

Mean size

Analysis of mean size per reef indicated a significant Method*Region*Zone effect ($F_{3,8} = 6.68$, $P = 0.012$). The mean sizes of the samples taken by hook-and-line were consistently higher than those taken by spear fishing in all regions and management zones (Table 1; Fig. 1). The significant interaction indicated that the relative magnitude of bias of the methods depended on zone or region, or both and that inferences about the effects of zone and region varied depending on the method used to gather the data. Line-caught *P. leopardus* were, on average, significantly longer on no-take reefs than on fished reefs in the Townsville, Mackay and Storm Cay regions but not in the Lizard Island region (Fig. 1). Speared *P. leopardus* were longer, on average, on the no-take reefs in Townsville and Mackay regions but not in the Storm Cay or Lizard Island regions (Fig. 1).

Table 1. Numbers of fish sampled (*n*), mean size (fork length, FL) and age, and the size and age ranges for samples collected by each method for each region and management zone

Standard errors for each of the means are given in parentheses. LI, Lizard Island; MKY, Mackay; SC, Storm Cay; TVL, Townsville

Method	Region	Zone	*n*	Mean size (FL in mm)	Mean age (years)	Size range (FL)	Age range (years)
Spear	LI	Fished	294	325.9 (5.4)	3.1 (0.1)	126–540	1–9
Spear	LI	No-take	253	359.3 (5.6)	4.3 (0.1)	157–603	1–16
Spear	TVL	Fished	159	342.0 (6.6)	2.9 (0.1)	176–522	1–8
Spear	TVL	No-take	99	414.0 (8.4)	4.3 (0.2)	216–557	1–11
Spear	MKY	Fished	277	296.2 (4.6)	2.6 (0.1)	149–610	1–10
Spear	MKY	No-take	270	348.4 (6.0)	3.5 (0.1)	128–596	1–11
Spear	SC	Fished	307	325.1 (4.9)	3.8 (0.1)	121–629	1–16
Spear	SC	No-take	310	339.6 (5.4)	3.9 (0.1)	108–685	1–14
Line	LI	Fished	273	400.8 (4.2)	4.7 (0.1)	257–600	1–15
Line	LI	No-take	247	406.5 (5.1)	5.6 (0.1)	292–633	2–16
Line	TVL	Fished	104	409.6 (6.1)	3.9 (0.1)	275–558	1–9
Line	TVL	No-take	161	448.3 (4.5)	5.3 (0.2)	293–575	1–11
Line	MKY	Fished	303	375.9 (3.0)	4.4 (0.1)	269–628	2–10
Line	MKY	No-take	496	428.2 (3.1)	5.1 (0.1)	270–662	2–13
Line	SC	Fished	317	370.6 (3.7)	4.9 (0.1)	250–630	2–15
Line	SC	No-take	470	413.6 (2.9)	5.6 (0.1)	276–630	1–13

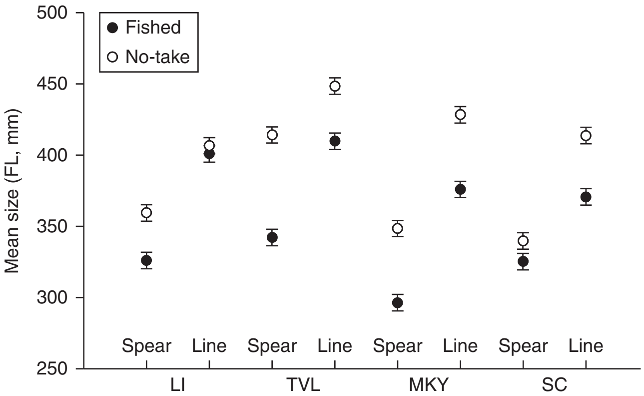


Fig. 1. Regional and zonal patterns in mean size (FL, mm) of *Plectropomus leopardus* taken in fished (dark symbol) and no-take (light symbol) zones by spear and line fishing from the Lizard Island (LI), Townsville (TVL), Mackay (MKY), and Storm Cay (SC) regions. Error bars are standard errors.

Similarly, inferences about differences among regions for fished reefs differed with method. Hook-and-line caught *P. leopardus* were of similar size on fished reefs in the Townsville, Lizard Island, and Mackay regions, while fish from the Storm Cay region were of similar size to those from Lizard Island and Mackay regions but smaller than Townsville fish (Fig. 1). *P. leopardus* speared on fished reefs were not significantly different in length among the Lizard Island, Townsville, or Storm Cay regions but fish from the Mackay region were significantly smaller than those from Townsville (Fig. 1). Regional patterns in the size of fish on no-take reefs were superficially similar for both methods, although the hook-and-line data indicated that the Townsville region had significantly larger fish than the Lizard Island region only whilst the spear fishing data indicated that the Townsville fish were significantly larger on average than fish from all other regions (Fig. 1).

Mean age

The effects of Method*Region*Zone, Method*Region and Method*Zone on mean age were all non-significant ($F_{3,8} = 1.21$, $P = 0.367$; $F_{3,8} = 3.75$, $P = 0.060$; $F_{1,8} = 0.039$, $P = 0.849$, respectively), indicating that any difference in mean age between the two methods was consistent across regions and management zones. The main effects of Method and Zone did influence mean age (Method, $F_{1,8} = 143.88$, $P \ll 0.001$; Zone, $F_{1,8} = 11.69$, $P = 0.009$) but Region did not ($F_{3,8} = 0.772$, $P = 0.541$). The mean age estimated from the speared sample (3.51 ± 0.046 s.e.) was significantly lower than that from the line sample (5.03 ± 0.038 s.e.). The mean age estimated from the fished zone (3.85 ± 0.041 s.e.) was significantly lower than from the no-take zone (4.78 ± 0.045 s.e.) averaged over both methods and all regions. The range in ages sampled by each method was 1–16 years, although 1-year-old fish were rarer in the line-caught samples (Table 1).

Population size structure

The size range of fish sampled by hook-and-line was 250–662 mm, while for spear fishing it was 108–685 mm (Table 1). The best-fit log-linear model to describe the size structure data contained all main effects and all interaction effects. The effect of the four-way interaction was significant (L-R, $\chi^2_{24} = 39.072$, $P = 0.027$). Fitting the Method*Zone*Size models to each region indicated that zone significantly affected the size structures taken by each method in the Storm Cay region only (Method*Zone*Size, L-R, $\chi^2_8 = 35.096$, $P < 0.001$). There was a significant effect of method on size class frequencies in each zone (Method*Size (fished, $\chi^2_8 = 74.147$, $P < 0.001$; no-take, $\chi^2_8 = 199.794$, $P < 0.001$)). The significant effect of method in the fished zone was removed by omitting the <310-mm size class ($\chi^2_7 = 6.198$, $P = 0.517$). The effect of method was removed in the no-take zone after removal of the <310-mm and the 310–340-mm size classes ($\chi^2_6 = 10.315$, $P = 0.112$). Spear fishing caught significantly more fish <310 mm in the Storm Cay fished and no-take zones and significantly more fish in the 310–340-mm size class in the no-take zone than hook-and-line (Fig. 2*g*, *h*). There was a significant effect of zone on size class frequencies for each method but the effect was more evident in the line sample (Zone*Size (Spear, $\chi^2_8 = 23.198$, $P = 0.003$; Line, $\chi^2_8 = 152.187$, $P < 0.001$)). The significant effect was removed in the spear-caught samples by omitting the 310–340-mm and the 400–430-mm size classes ($\chi^2_6 = 11.607$, $P = 0.071$), though omitting the 310–340-mm and the 340–370-mm size classes produced a similar result ($\chi^2_6 = 11.899$, $P = 0.064$) (Fig. 3*a*). The significant effect for the line-caught samples was removed by omitting the three smallest size classes ($\chi^2_5 = 8.050$, $P = 0.154$) (Fig. 3*b*).

Fitting the Method*Region*Size models to data from each zone indicated that Region significantly affected the size structures taken by each method in both the fished and no-take zones (Method*Region*Size (L-R, $\chi^2_{24} = 53.026$, $P = 0.001$, and L-R, $\chi^2_{24} = 66.654$, $P < 0.001$, respectively)). Removal of the <310-mm size class from samples from the fished zone achieved similar frequency distributions between methods in the Lizard Island, Townsville, and Storm Cay regions (Method*Size (Lizard Island, $\chi^2_7 = 12.714$, $P = 0.079$; Townsville, $\chi^2_7 = 12.499$, $P = 0.085$; Storm Cay, $\chi^2_7 = 6.198$, $P = 0.517$) (Fig. 2*a*, *c*, *g*), whilst removal of both the <310-mm and 310–340-mm size classes was required to remove the effect of method on frequency distributions in the Mackay fished zone (Method*Size: $\chi^2_7 = 7.466$, $P = 0.280$) (Fig. 2*e*). No significant differences among size frequencies between methods was achieved by removing the <310-mm size class from no-take zone data in both the Lizard Island and Townsville regions (Lizard Island, $\chi^2_7 = 13.208$, $P = 0.067$; Townsville, $\chi^2_7 = 13.570$, $P = 0.059$) (Fig. 2*b*, *d*), removing the two smallest size classes in the Storm Cay region ($\chi^2_6 = 10.315$, $P = 0.112$) (Fig. 2*h*), and removing the three smallest size classes in the Mackay region ($\chi^2_5 = 7.816$, $P = 0.167$) (Fig. 2*f*).

A Chi-square test of Region*Size was done for each method in each zone to assess what the differential sampling bias would mean for inferences about the effect of region on size distribution. There was a significant effect of region on size class frequencies for each method (Table 2). The significant effect was removed from the spear-caught samples in the fished zones by omitting the Mackay region, while for the hook-and-line sample in the fished zones, both the Storm Cay and Mackay regions or both the Lizard Island and Townsville regions needed to be removed (Fig. 4; Table 2). The significant effect was

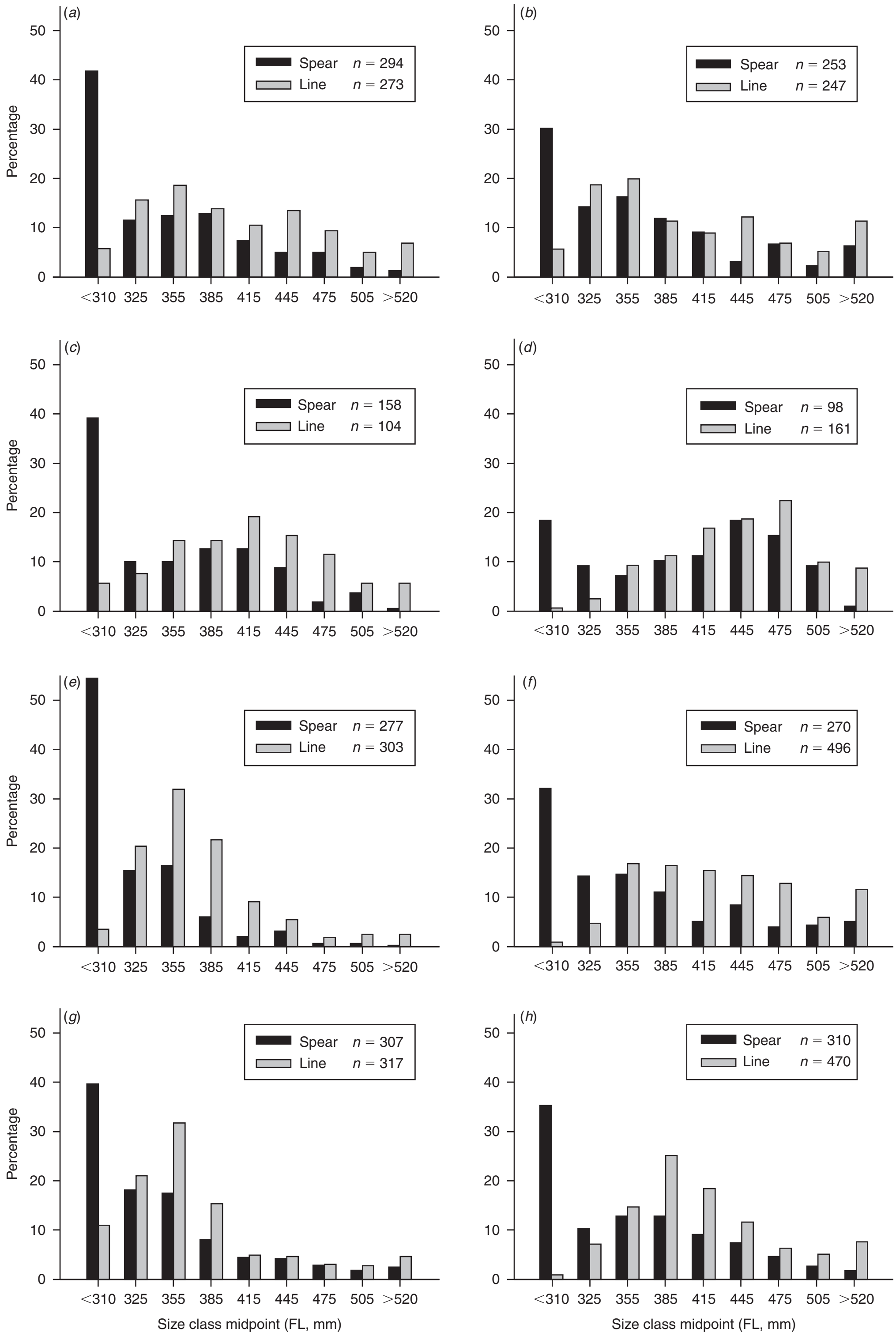


Fig. 2. Frequency (%) of *Plectropomus leopardus* in 30-mm size classes from <310 to >520 mm, from the spear- (dark bars) and line-caught (light bars) samples for each of the fished (left column) and no-take (right column) zones. Horizontal axis labels between 310 and 520 are midpoints of each size class (mm). Figure rows from the top represent the (*a*, *b*) Lizard Island, (*c*, *d*) Townsville, (*e*, *f*) Mackay, and (*g*, *h*) Storm Cay regions, respectively. *n* = sample size.

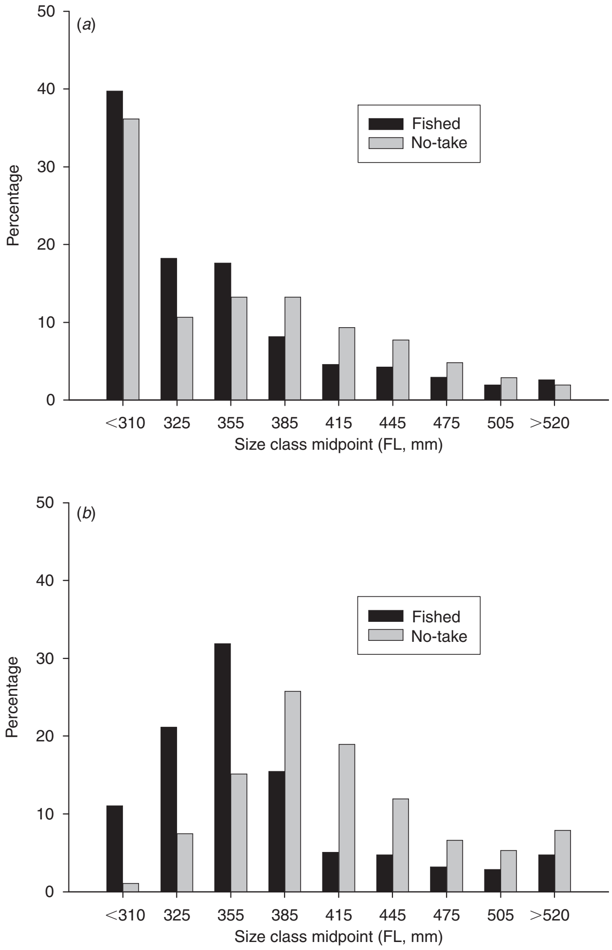


Fig. 3. Frequency (%) of *Plectropomus leopardus* in 30-mm size classes from <310 to >520 mm from the fished (dark bars) and no-take (light bars) zones from the Storm Cay region, for samples collected by the (*a*) spear and (*b*) line method. Horizontal axis labels between 310 and 520 are midpoints of each size class (mm).

removed in the no-take zones by omitting the Townsville region from the spear-caught samples and removal of either the Lizard Island and Storm Cay regions or the Lizard Island and Townsville regions from the line-caught samples (Table 2).

Population age structure

The best-fit log-linear model to describe the age data contained the three-way interaction terms Method*Region*Age, Method*Region*Zone, and Region*Zone*Age (L-R, $\chi^2_{24} = 22.925$, $P = 0.524$). The term Method*Region*Zone reflected patterns in sample size (abundance) unrelated to age and likely to reflect the relative sampling efficiencies (catch per unit effort: CPUE) of the different gears and thus were not investigated further. As the interaction of Region*Zone*Age was unrelated to sampling method, it was not explored further.

The significant three-way interaction of Method*Region*Age (L-R, $\chi^2_{18} = 49.964$, $P < 0.001$) indicated potential influences of Region on the interaction between Method and Age (effectively, the relative age-related bias of the methods). All regions showed significant effects of method on age class frequencies when considered separately (Method*Age (Lizard Island, $\chi^2_6 = 210.168$; Townsville, $\chi^2_6 = 85.252$; Mackay, $\chi^2_6 = 453.265$; Storm Cay, $\chi^2_6 = 328.817$; all regions $P < 0.001$)). Removal of the <3-, 3-, and 6-year age classes from the Lizard Island samples (Fig. 5*a*) greatly improved agreement between the age class frequencies of the two methods ($\chi^2_3 = 6.964$, $P = 0.073$). A similar result was found in both the Mackay and Storm Cay regions except the 7-year and ≥7-year fish, respectively, also had to be removed before the age distributions from the two methods did not differ significantly (Mackay, $\chi^2_2 = 2.727$, $P = 0.256$; Storm Cay, $\chi^2_2 = 5.999$, $P = 0.050$) (Fig. 5*c*, *d*). The difference between samples for the older age classes was not as large in the Townsville region and a method-independent best fit to the data was obtained by removing only the <3- and 3-year-olds ($\chi^2_4 = 6.162$, $P = 0.187$) (Fig. 5*b*).

Chi-square tests of Region*Age were done separately for each method in each zone to assess what the differential bias in

Table 2. Summary of inferences made about regional patterns of size structure of samples taken by hook-and-line fishing and spear fishing from fished and no-take management zones

LI, Lizard Island; MKY, Mackay; SC, Storm Cay; TVL, Townsville

Test	χ^2_{18}	*P*-value	Pattern
Spear 'fished'	79.57	<0.001	MKY / LI TVL SC
All regions	36.27	0.052	
MKY removed			
Line 'fished'	123.20	<0.001	LI TVL / MKY SC
All regions	9.54	0.996	
SC and MKY removed	22.32	0.560	
TVL and LI removed			
Spear 'no-take'	73.60	<0.001	TVL / LI MKY SC
All regions	28.12	0.255	
TVL removed			
Line 'no-take'	148.16	<0.001	LI / TVL MKY SC
All regions	21.06	0.635	
LI and SC removed	29.71	0.195	
LI and TVL removed			

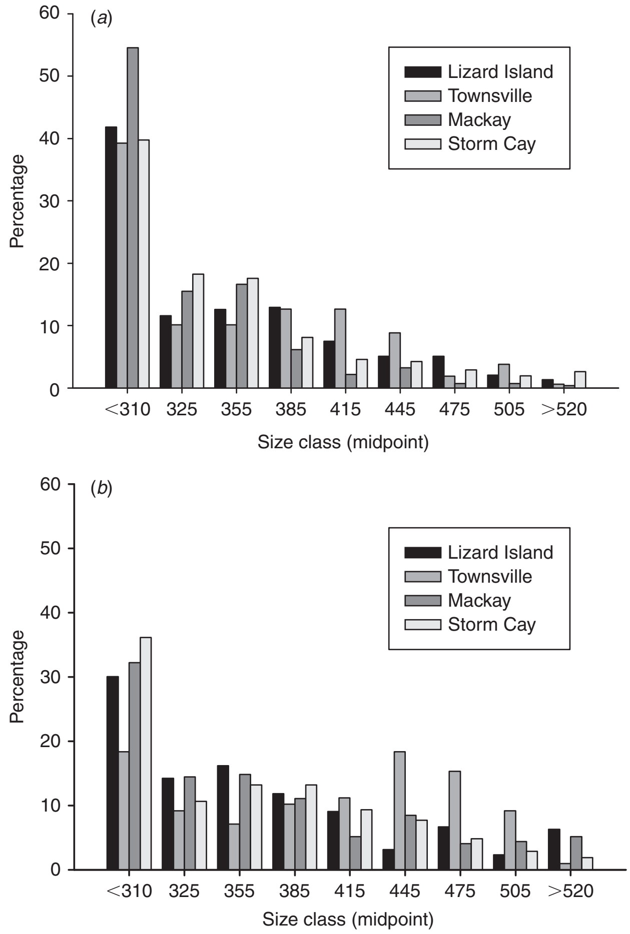


Fig. 4. Frequency (%) of *Plectropomus leopardus* in 30-mm size classes from <310 to >520 mm from the Lizard Island, Townsville, Mackay and Storm Cay regions for samples collected in the fished zones by (*a*) spear and (*b*) line fishing. Horizontal axis labels between 310 and 520 are midpoints of each size class (mm).

method would mean for inferences about the effect of region on age distribution. There was a significant effect of region on age frequencies for each method (Table 3) but the regional patterns differed between the methods. The inference from the spear samples from the fished zones was that the Storm Cay, Lizard Island and Townsville regions were similar and the Mackay and Townsville regions also were similar. The line sample data, however, indicated that the Lizard Island, Mackay and Storm Cay regions were all similar, as were the Townsville and Lizard Island regions (Table 3). In the no-take zones, the spear sample found the Townsville, Lizard Island, and Storm Cay regions to be similar but the Mackay region was also similar to Lizard Island and Storm Cay regions. The line sample data grouped the Townsville, Lizard Island and Storm Cay regions as being similar and also indicated that the Mackay and Storm Cay regions were similar (Table 3). In most cases, Townsville and Lizard Island regions were similar, while Mackay was generally the most dissimilar to other regions.

Discussion

Sampling gear selectivity

The greatest difference in the samples taken by spear fishing and hook-and-line occurred in the amounts and proportion of smaller and younger fish. Fish less than 310 mm and younger than 4 years, and 1- and 2-year-old fish in particular, comprised a larger proportion of the speared than the line sample on most reefs, regardless of regions or management zone, thereby supporting our hypothesis that hook-and-line fishing under-samples smaller and younger fish. The hypothesis that hook-and-line fishing may sample relatively more larger fish was also supported, though not as pronounced, whereby hook-and-line sampled more fish in the larger size classes (>370 mm) and older age classes ($\geq$6 years) relative to spear fishing. More importantly, our primary null hypothesis that any sampling biases would be unaffected by either region, management zone, or their interaction was not rejected. That is, the sampling biases observed were qualitatively consistent in all regions and management zones. These different biases resulted in significantly lower mean sizes and ages of fish in the speared samples.

Brown *et al.* (1996) noted similar differential biases between speared and line-caught *P. leopardus* on the GBR. Elsewhere on other species, the use of different sampling gears has also resulted in different portions of populations being sampled, resulting in different size- and age-related estimates of population parameters (e.g. DeVries 2007; Wells *et al.* 2008). More effective sampling of larger and older fish by hook-and-line in this study, although relatively slight, possibly reflected the fact that this method sampled at greater depths, down to 30 m. Spear sampling, in contrast, was restricted to <10 m depth. Larger, and usually older, fish often are found in deeper water (Morales-Nin and Ralston 1990; Mapstone *et al.* 2001; Collins *et al.* 2007). It is also possible that larger fish are disproportionately sampled by hook-and-line through competition for baits (Hovgard and Riget 1992). Larger home-range areas of larger fish (Samoilys 1997; Zeller 1997) may also increase exposure of larger fish to capture by hook-and-line gear. The authors have observed on several occasions that larger *P. leopardus* chase smaller individuals away from baits. Further, St John *et al.* (2001) reported that *P. leopardus* are cannibalistic and so it is likely that smaller fish will avoid larger individuals, reducing their tendency to take baits when large individuals are present. Also, cautious behaviour towards divers by larger fish may make them harder to spear.

Age distributions of samples from both gears, in all regions and zones, had a mode at age 4 years, but the age distributions from speared samples also consistently had a mode in the <3 years class. It is not possible to determine here, however, whether 1- or 2-year-old fish were fully recruited to the spear fishing gear. The single mode at age 4 years in the line-caught samples indicates full selection of *P. leopardus* was likely to be at age 4 years, consistent with previous work (Strachan-Fulton 1996) but a second mode at age 4 years in the spear sample also suggests that this age class may have been an unusually strong year class. Large variation in annual settlement is widely documented in several fish species (e.g. Duffy-Anderson *et al.* 2005) and it has been noted on the GBR that this variation can influence strongly population structure and

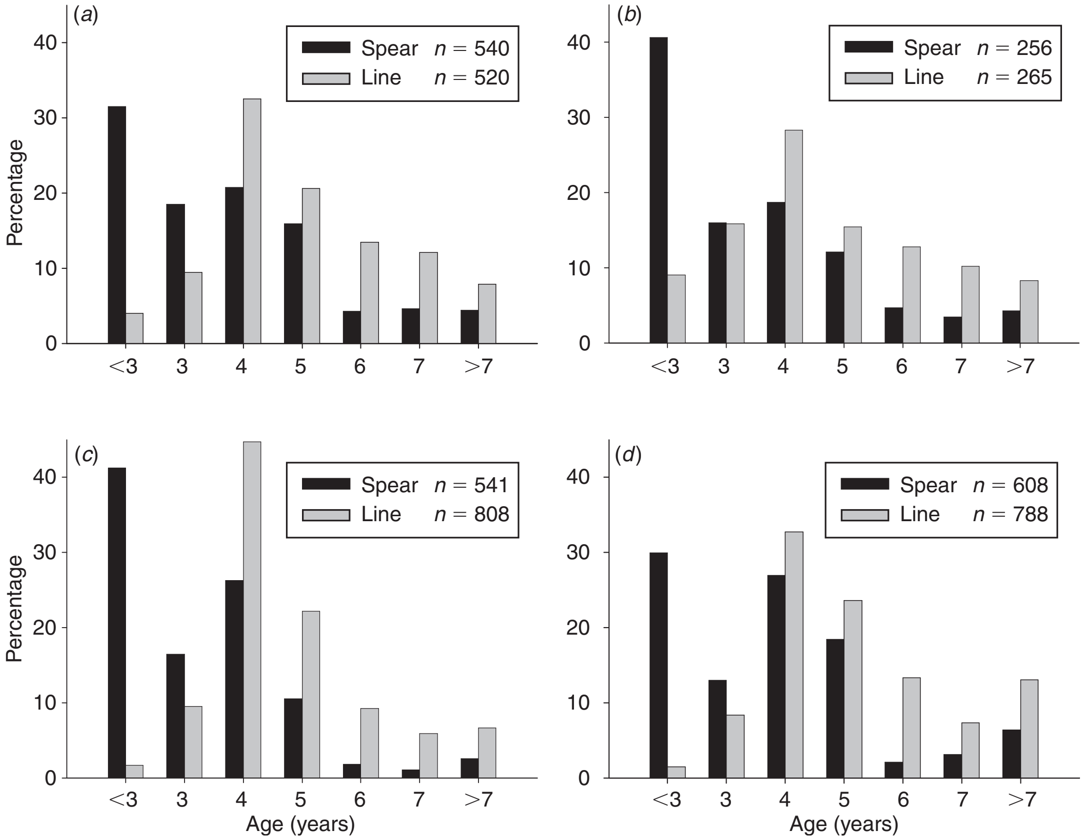


Fig. 5. Frequency (%) of *Plectropomus leopardus* in each age class (years) for each of the speared sample (dark bars) and the line sample (light bars) from the (*a*) Lizard Island, (*b*) Townsville, (*c*) Mackay, and (*d*) Storm Cay regions.

abundance of *P. leopardus* (Ferreira and Russ 1995; Brown *et al.* 1996; Russ *et al.* 1996, 1998). The hypothesis that the strong 4-year-old cohort in both spear and line samples was possibly settlement-driven was supported by unusually high catches of larval *P. leopardus* in light traps in the Cairns region in the 1991–92 austral summer (Doherty 1996). Ayling and Ayling (1997) also recorded unusually high counts of very small *P. leopardus* in underwater visual surveys on reefs near Townsville in early 1992. The strong 4-year-old cohort was evident over a very large area of the GBR (7° latitude), suggesting a settlement pulse in 1991–92 over a wide geographic range. Interpretation of the line data alone would likely have failed to recognise the potential prior settlement pulse and have simply interpreted that 4 years was the age of full recruitment to the gear.

These results provide a clear demonstration of gear-specific size selectivity. The selectivity curve developed by Strachan-Fulton (1996) for hook-and-line gear targeting *P. leopardus* on the GBR (using data from this study) showed an increase in selectivity (probability of capture) with size to full recruitment to the line gear at ~390 mm FL (fork length), with constant selectivity above that size. Very few fish were captured below 290 mm FL (selectivity $\approx$ 0.20) and almost none below 230 mm (Strachan-Fulton 1996). Fish less than 310 mm comprised 3.92% of the line-caught sample but 38.18% of the spear-caught sample in this study. The smallest speared individual was 108 mm FL. The difference in relative numbers of fish <310 mm taken by spear and hook-and-line emphasised the limitations of hook-and-line with commercial-grade gear to adequately sample smaller and presumably younger fish. This is a significant and common issue in fisheries sampling, especially where parameters of growth are to be derived from the sample (Hilborn and Walters 1992).

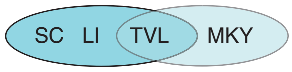
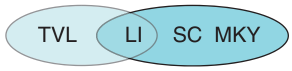
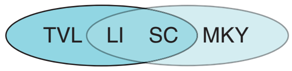
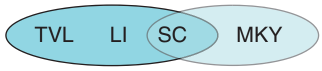
Although spear fishing appeared to take a more representative length and age sample of *P. leopardus*, it is likely that spear fishing also under-sampled smaller fish and perhaps very large fish. The pilot study done to develop the spear fishing target selection protocol for this work suggested that spear fishing under-sampled fish <200 mm by ~25% compared with underwater visual surveys (D. Welch, unpubl. data). Juvenile *P. leopardus* have cryptic behaviour after settlement, often occupying inaccessible habitats (Doherty *et al.* 1994) that would reduce the likelihood of them being speared.

Sampling gear effects among management zones

More small fish (<310 mm) and young fish (<4 years) were captured by both methods in the fished relative to the no-take zone in most regions. In contrast, more large (>400 mm) and old fish ($\geq$6 years) were captured in the no-take than fished zones by both spear and hook-and-line. *P. leopardus* is relatively

Table 3. Summary of inferences made about regional patterns of age structures of samples taken by hook-and-line fishing and spear fishing from fished and no-take management zones

LI, Lizard Island; MKY, Mackay; SC, Storm Cay; TVL, Townsville

Test	χ^2_{18}	*P*-value	Pattern
Spear 'fished'	82.49	<0.001	
All regions	5.23	0.998	
SC and LI removed	8.64	0.968	
SC and MKY removed	25.97	0.101	
MKY and TVL removed	28.67	0.053	
MKY and LI removed			
Line 'fished'	85.52	<0.001	
All regions	12.77	0.805	
TVL and MKY removed	23.38	0.176	
MKY and SC removed	25.88	0.103	
TVL and SC removed	28.30	0.058	
LI and TVL removed			
Spear 'no-take'	44.15	<0.001	
All regions	26.72	0.084	
MKY removed	28.40	0.056	
TVL removed			
Line 'no-take'	69.14	<0.001	
All regions	7.46	0.986	
MKY and SC removed	20.42	0.310	
TVL and MKY removed	22.05	0.230	
LI and MKY removed	23.58	0.169	
LI and TVL removed	27.62	0.068	
LI and SC removed	28.70	0.052	
TVL and SC removed			

sedentary (Zeller 1997) and fishing on open reefs would be expected to truncate the upper size and age distributions of populations there compared with those in no-take zones (Roberts and Polunin 1991; Willis *et al.* 2003; Lester *et al.* 2009). The greater proportion of smaller fish in fished zones may indicate a secondary effect of fishing, either through reduction of cannibalism of small fish (St John *et al.* 2001) or through density-dependent settlement compensation at reduced population density. Greater proportions of small coral trout on fished than no-take reefs on the GBR have been reported elsewhere from underwater visual surveys (Ayling *et al.* 1992; Mapstone *et al.* 2004) and line fishing (Mapstone *et al.* 2004). Hook-and line sampling may underestimate differences in size and age structure between zones if there are greater proportions of small fish in fished than no-take zones.

Statistical inferences about zoning effects and regional variation, however, varied with method and the metric analysed. Analyses from both methods indicated that no-take zones in the Mackay region had significantly higher mean sizes of fish than the fished zones, whilst only the line-caught samples indicated a similar result in the Storm Cay region. Fishing effort in both regions is amongst the highest on the GBR (Mapstone *et al.* 1996*b*) and so any effects of no-take areas would be expected in these regions. A high proportion of fish <310 mm was caught by spear fishing in both the fished zone (39.74%) and no-take zone (36.13%) in the Storm Cay region, however, resulting in similar mean sizes between zones. The overall high catch of small fish may have reflected a strong recent recruitment pulse in this region because in spear samples from all other regions there were appreciably more fish <310 mm in the fished zone than in no-take zones. Alternatively, the Storm Cay region may have a more complex physical habitat that provided protection from predators and enhanced survivorship of smaller fish.

Samples from the different gears also resulted in different inferences of zone effects in the Townsville region. There, the speared samples indicated a significantly greater mean size, with fewer fish <310 mm, in the no-take zone than the fished zone. No statistically significant difference was observed in mean size between zones based on the line samples, however, despite there being an apparent difference in mean size and the no-take size distribution showing a shift to the right. Fishing effort in the Lizard Island region has been the lowest historically of all the regions sampled (Mapstone *et al.* 1996*b*) and no statistical difference was found between zones in the mean size and size structures for samples from either gear. This perhaps reflects a lesser effect of fishing than in other regions and, accordingly, a reduced consequence of protection from fishing in the no-take zones. Effects of zoning were evident on the age structures that were consistent for each method, with generally more young fish in fished zones and more old fish in no-take zones and correspondingly higher mean age in no-take zones than in fished zones. This consistency contrasts with variation in zone effects on size and suggests that analyses of age may be less sensitive than analyses of size to differential gear selectivity.

Sampling gear effects among regions

Regional differences in population size structure have been documented for reef fishes globally (e.g. Williams 1991; Lombardi-Carlson *et al.* 2008). Regional patterns in both mean size and size structure we inferred differed between the two methods and also differed depending on whether sampling was on fished or no-take reefs. Despite this variation, however, mean size in the Townsville region tended to be greater than in other regions in samples from both methods. There were fewer small fish in the Townsville region in both the spear and the line samples, suggesting that recruitment there may have been low relative to the other regions sampled. This was also suggested by lower catches of 1-year-old fish in the Townsville region in the spear sample. The modal size class above 310 mm in the Townsville samples was also larger than elsewhere, being 460–490 mm compared with 340–370 mm in all other regions. The reefs we sampled in the Townsville region are more exposed to the oceanic waters of the Coral Sea than those in the other regions sampled in this study and are characterised by steep reef edges, clear water, and few off-reef structures such as isolated bommies. Reefs in the other three regions are different and have more gently sloping reef edges, more turbid waters, and more complex and extended off-reef structures. These factors may account for apparently lower recruitment in the Townsville region, given that *P. leopardus* settle preferentially to shallow rubble habitat (Light and Jones 1997).

Implications of sampling effects

Size-based methods of fisheries' stock assessments use size as a proxy for age, making them especially vulnerable to size-selective biases in sampling gears. Smaller, younger fish are expected to dominate populations numerically and their absence or under-representation in samples is particularly likely to bias assessments of population harvest potential (Hilborn and Walters 1992). Our work indicates that the spear sample provides a better representation of these smaller and younger fish in populations of *P. leopardus*. The inability of hook-and-line to sample these fish representatively overestimates mean sizes and ages. Setting catch quotas based on such estimates could very quickly result in over-harvesting of stocks (Hilborn and Walters 1992).

The greater ability of spear fishing to sample 1-, 2- and 3-year-old fish compared with hook-and-line means that spear estimates of mean age will be consistently lower. It also indicates that estimates of mean age from hook-and-line samples should be explicitly considered only as 'mean age of the catch'. This feature of the spear fishing method also means that speared samples better identify strong or weak year-classes before they become vulnerable to the fishery. Early detection of strong or weak year-classes can help planning of future management of the fishery, especially where regulation is by annually reviewed catch or effort quotas (Russ *et al.* 1996). Underwater visual survey methods could also be useful in predicting good or poor fishing years by counting the young fish before recruitment to fishing gears or legal harvest sizes. Such non-destructive methods, however, are unable to give estimates of age for fish older than the newly settled juveniles, where specific age–size associations are blurred early in life (as is the case for *P. leopardus*) or to provide data on other biological parameters such as sex.

Many studies globally have documented gear selectivity by comparing the performance of different sampling gears in deriving population metrics such as size (e.g. Wells *et al.* 2008). Several studies have documented regional variation in fish populations (e.g. Lombardi-Carlson *et al.* 2008) and the efficacy of fishery no-take management zones (e.g. Willis *et al.* 2003; Lester *et al.* 2009). However, this appears to be the first experimental study that examines how different sampling gears may influence the inferences made about spatial population differences or about the effects of fishing on populations. Selectivity and bias of hook-and-line gear has been widely considered but poorly understood (Ralston 1990). Here we demonstrate the potential magnitude in sampling bias for what is a commonly used fish sampling tool for ecological and fisheries studies worldwide.

This study represents the first examination of this selectivity and bias over large spatial scales (7° of latitude) or between no-take and fished zones. Our results indicate that assessment of no-take reserve effects may be influenced significantly by the gear employed to sample them and neighbouring areas. Similarly, inferences of regional patterns in population structure also may be sampling gear-dependent, especially where a gear largely fails to sample significant parts of populations. This is important because it indicates that comparisons of size and age among regions of different physical and environmental characteristics, or between areas subjected to or protected from fishing, may be susceptible to relatively subtle changes in gear effects. Accordingly, we recommend careful consideration of sampling bias and its interaction with other effects, such as density, management arrangements, fishing, and spatial patterns in populations, when drawing conclusions about the impacts of such effects based on samples that are known to be only a subset of the underlying population.

Acknowledgements

We thank Lizard Island Research Station, the crews of 'Whyllaway', 'Hamdon Star' and 'RV James Kirby', Judy Horsfall, Matt Kenway, and members of the Townsville Skindiving Club, particularly Bill Roberts and John Robinson, for assisting in the field collections. Ashley Williams (AW in Methods) assisted with otolith counts. The CRC Reef Research Centre is acknowledged for the financial support. We are grateful for the constructive comments received from the Editor, Professor Andrew Boulton, and two anonymous referees. Sampling work was conducted under the following permits: GBRMPA permits G96/454, QFMA Permit No. 42294, and JCU Ethics approval No. A771_02. This manuscript is a contribution from the Co-operative Research Centre's Reef Effects of Line Fishing Project.

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Manuscript received 2 November 2009, accepted 27 April 2010