

**Space utilization  
characteristics  
of snapper (*Pagrus auratus*)  
in a  
marine reserve**



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Report to the Department of Conservation  
November 2000

## **Executive Summary**

The movements of five acoustically tagged *Pagrus auratus* in the Cape Rodney-Okakari Point Marine Reserve were tracked over a five month period. During this time, all fish showed a high level of site fidelity to particular areas of reef, with the widest ranging fish having a core area of 300m<sup>2</sup>. Additional analysis of the five fish revealed a degree of individual variation that represents a spectrum of site attached behaviour. The observed spatial ranges of these fish were not different from short-term data from thirteen *P. auratus* monitored after voluntarily ingesting transmitters. The space utilization patterns from one of these thirteen fish is presented here. Seasonally, movement patterns varied little between February (summer) and May (winter). However, each fish was observed to make excursions to the same non-core area during February and up to 16% of their time was spent in this area. We tentatively suggest that offshore reserve boundaries are placed at a distance of at least 540 m from the edge of any reef structure in order to fully protect resident snapper.

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## Introduction

Some of the potential benefits of marine reserves are to increase abundance and size of animals within them, increase recruitment and sustain genetic diversity of targeted species (Dugan & Davis 1993). Increased abundance and size of fish species due to reserve protection has been demonstrated (Bennett & Attwood 1991, Millar & Willis 1999) but direct proof of such effects are rare (Willis & Babcock 1998b). Demonstration of effects on recruitment and genetic diversity will require studies on much larger spatial and temporal scales than those that have been conducted to date. A further potential benefit is the emigration of targeted species to fished areas adjacent to reserves. Such emigration would justify their use not only for conservation but also as fisheries management tools on much more accessible spatial and temporal scales (Alcala & Russ 1990, Attwood & Bennett 1994, Alison *et al.* 1998, Kramer & Chapman 1999). This has only been described once. When the collapse of reserve protection at Sumilon Is. in the Philippines resulted in a reduction of catch per unit effort (CPUE) in previously fished adjacent areas (Russ & Alcala 1996). Despite this lack of evidence marine reserves remain a popular option as a supplement to existing fisheries regulations., Compared to mainstream fisheries control regulations, such easy and cheap management makes marine reserves an attractive tool (Dugan & Davis 1993).

Marine reserve effectiveness can be optimised by designing spatial configuration (i.e. size, shape and habitats) to ensure the protection of the most important recreational and commercial target species. Information on movement patterns, activity and home range size of the species concerned is considered very important to reserve design (Roberts & Polunin 1991, Attwood & Bennett 1994, Holland *et al.* 1996, Zeller 1997, Alison *et al.* 1998, Woodroffe & Ginsberg 1998, Kramer & Chapman 1999, Willis *et al.* 2000). Traditionally such information has been gathered through mark and recapture studies. Such studies have shortcomings, such as the restriction to usually one recapture locality for each fish (Zeller 1999). Advances in technology have allowed more detailed behavioural studies to take place. With the advent of ultrasonic telemetry individual fish can be continuously tracked for reasonable periods of time. It is important that such fine scale monitoring is

backed up with more traditional long term tagging of a larger sample size of fish (Willis *et al.* in press).

The New Zealand snapper (*Pagrus auratus*: Sparidae) is one of the most important recreational and commercial fish species in New Zealand (Annala & Sullivan 1996). A surprisingly small amount of research has been conducted on the movement patterns of *P. auratus*. Fishermen and scientists alike have long believed that *P. auratus* follow a seasonal migration into shallow water (Cassie 1956, Crossland 1976). This is commonly referred to as the 'schooling snapper theory'. It is believed that such movement is related to water temperature or the formation of spawning aggregations (Paul 1976). This theory is somewhat at odds with observed build-up of *P. auratus* abundance in the Cape Rodney-Okakari Point Marine Reserve (hereafter referred to as the CROP reserve) (Willis *et al.* 2000). This build-up and the spatial distribution of *P. auratus* within the reserve (Willis *et al.* 2000), is more consistent with the alternative theory, that a proportion of *P. auratus* are year round residents on reefs (the 'Kelpie' theory).

Other techniques have also been used in the CROP Reserve to study *P. auratus* movement. Visible implant fluorescent elastomer (VIFE) tags have been assessed and found to be a useful tool for monitoring the movement of *P. auratus* (Willis and Babcock 1998a). So far results show site attachment to an area of only a few hundred metres over a period of greater than three years (Willis *et al.* in press). This strong evidence for site attachment, as opposed to long held beliefs that *P. auratus* are a wide-ranging species, appears to be a contradiction. However, work on galjoen (*Coracinus capensis*) has shown that within a species more than one fish dispersion pattern is possible (Attwood and Bennett 1994). The importance of such information to sustainable fisheries management has been realized in Shark Bay, Western Australia where *P. auratus* exhibit both resident and mobile behaviour in a small geographic region, resulting in separate management of the two stocks (Moran 1987).

The site of this study is the Cape Rodney-Okakari Point (CROP) Marine Reserve. By use of angling surveys and baited underwater video (BUV), the abundance of *P.*

*auratus* in the reserve was found to peak at the centre, and declined towards the edges of the reserve (Millar & Willis 1999, Willis *et al.* 2000). There are two possible explanations for this pattern. One is the lack of surveillance towards the reserve edges, which would make poaching without detection an easier task there. Alternatively as distance to the reserve edge decreases, the chance of a *P. auratus* home range overlapping the boundary increases. Therefore high levels of fishing on the edge of the CROP Reserve could explain the gradual decrease in *P. auratus* abundance from the reserve centre, and are consistent with the limited scale of movement suggested by VIFE tagging studies.

## **Materials and Methods**

### *Experimental area and procedure*

This study was conducted in the CROP reserve from January to June 2000. During this time *Pagrus auratus* (snapper) were continuously tracked via the use of a radio-acoustic positioning and telemetry system (RAPT). This system allowed accurate positioning ( $\pm 1-2\text{m}$ ) of individual fish every five minutes. Each *P. auratus* monitored contained a transmitter set to an individual frequency, eliminating confusion between tagged fish. The ultrasonic signal transmitted from each fish was then received by three moored sono-buoys that triangulated the position of the fish by differences in arrival time of the signal. The sono-buoys were placed in a triangular configuration approximately 300m apart, within Goat Island Bay (Fig. 1). This area was chosen for its high abundance of *P. auratus*, shelter, and the presence of shallow reef habitat suitable for *P. auratus*.

This study used V16 and V8 transmitters made by VEMCO electronics. The V8 transmitters ( $\sim 8\text{mm}$  diameter and 4.5cm length) were small enough to be swallowed by *P. auratus*. These transmitters were encased in bait and voluntarily ingested by *P. auratus*, *in situ*, without any handling. The transmitter would be retained for around two days before being passed. Once egested the transmitter could be found again, using a diver operated receiver (VUR96). The transmitter could then be recycled and fed to another *P. auratus*. This allowed smaller fish to be tracked, increased total sample size and allowed

a comparison of behaviour between surgically treated and undisturbed fish. A total of thirteen *P. auratus* from ~250mm to 500mm FL and one *Parapercis colias* (~300mm FL) were monitored for around two days each by using this method. The V16 transmitters (~16mm diameter and 7.5cm length) had a battery life conservatively estimated at 120 days (but were found to last much longer). A total of five *P. auratus* (Table 1) received surgically implanted transmitters. These V16 transmitters allowed long term, detailed monitoring of *P. auratus* movements.

**Table 1:** Transmitter frequency, fish size and tagging date of all snapper that received V16 transmitters.

<b>Transmitter Frequency</b>	<b>Snapper Size (FL mm)</b>	<b>Date Released</b>
60	426	24/1/00
54	415	24/1/00
57	532	24/1/00
63	400	30/1/00
50	515	4/2/00

Specimens of *P. auratus* were caught from the CROP reserve on hook and line to allow surgical insertion of the transmitter. All fish were caught using modified barbless hooks to reduce injury and the probability of ‘gut hooking’. Surgical procedures followed the methods described by Zeller (1997). After capture each fish was retained in an aquarium tank for 24 hours to reduce stress levels before surgical insertion of ultrasonic transmitters. Fish were anaesthetised with clove oil at  $0.27 \text{ M l}^{-1}$ , the maximum concentration used by Munday & Wilson (1997). After the fish had become immobile it was placed in a sponge cradle and the incision area was de-scaled and then sterilised with Tamodine (Vetark products). An incision approximately 2cm long was made 2-3cm anterior of the anus and the transmitter was then inserted into the gut cavity. The wound was then sutured with nylon suturing thread and each fish received an injection of tetracycline antibiotic (50mg/kg of fish). During surgery the gills were irrigated with

alternative doses of pure seawater and diluted anaesthetic to ensure the fish could still ventilate but remained unconscious. Each fish was then left to recover for at least 24 hours in an aquarium tank before release at the site of capture.

### *Data analysis*

Two weeks of monitoring data have been selected for analysis as being representative of the behaviour over the entire tagging period. The first of these periods ran from the 10<sup>th</sup> to the 17<sup>th</sup> of February while the second period ran from the 20<sup>th</sup> to the 29<sup>th</sup> of May. Spurious positional fixes due to background noise, signal reflection, turbulence and changing of sono-buoy batteries were removed from the dataset manually following the procedure employed by Lokkeborg *et al.* (2000). A positional fix was regarded as spurious if it was >50m from both its previous and successive fixes where these were close to each other.

Data were further analysed by dividing the total area tracked by the array into a grid composed of  $20 \times 20$  m bins. The time individual fish resided in each of these bins was then calculated using Matlab software. This required two assumptions: *i*) The fish swam in a straight line between consecutive positional fixes as long as these fixes were not more than 30 minutes apart; *ii*) The speed at which the fish swam between these two points was constant and equal to the distance divided by the time elapsed between two consecutive positional fixes. This allowed the location of the fish to be accounted for between fixes as long as the tracking system located the fish every 30 minutes.

## **Results**

### *Tagging and tracking system*

Movement of surgically tagged fish immediately after release from holding tanks was not noticeably different from that observed at any time afterwards. The transmitter signal from one *P. auratus* that received a surgical tag was observed to remain stationary shortly after release. The fish could not be found and it was assumed to have died due to



bacterial infection (observed prior to release). Any positional fixes obtained from this fish have not been included.

Behaviour of the 13 *P. auratus* that ingested V8 tags (Table 2) was very similar to that observed from fish that received tags via surgical implantation. Fish 78Khz, for example, with a fork length of 500mm, was tracked for around three days (Fig. 2) before passing its voluntarily ingested transmitter. Fish 78Khz utilized an area with a maximum diameter of 240 m and resided within an area of 180m<sup>2</sup> for 56.2% of this time (Table 3). These characteristics are consistent with those of the twelve other *P. auratus* that were fed transmitters, and do not appear to be drastically different to the space utilization characteristics expressed by *P. auratus* that received their transmitters surgically.

**Table 2:** Size and date of tagging for snapper that ingested V8 transmitters. Sizes were estimated visually by divers with an error of  $\pm 25$  mm.

<b>Snapper Size (FL mm)</b>	<b>Tagging date</b>
325	9/03/00
400	15/03/00
450	20/03/00
400	20/03/00
300	22/03/00
300	24/03/00
400	27/03/00
375	28/03/00
350	13/04/00
400	15/05/00
350	15/05/00
250	19/05/00
500	22/05/00

During the two periods of fish monitoring presented here, there were occasions when fish were not monitored for periods of up to five hours. This was due to loss of transmitter signal from the receptive field or shut-down of the monitoring system. Fish with core areas outside the centre of the sono-buoy array might also transmit a weaker signal to the monitoring system. Nevertheless, the large number of fixes at otherwise

frequent intervals indicated that nearly all movements of tagged fish were successfully monitored and that the core areas of each fish were represented accurately. The fact that each fish remained in almost exactly the same area (except fish 60 Khz) for a period greater than five months (Figs. 3 & 4), indicates that within the CROP reserve, these *P. auratus* are highly site-attached.

The behaviour of tagged fish did not appear to be unduly affected by human activities within the CROP reserve. Feeding of fish within the reserve had been actively stopped before this study began, and fish with surgically implanted transmitters would not allow divers to approach within visibility range (D. Parsons pers. obs.). Despite the cessation of hand-feeding by the public *P. auratus*, tagged or otherwise, remained in Goat Island Bay. While *P. auratus* still followed the glass bottomed boat and dive schools, tagged fish were never seen to be involved in such activity and observations of real-time tracking of fish gave no indication that tagged fish displayed such behaviour.

#### *Site fidelity*

The tracking system allowed us to build up a detailed picture of space utilization demonstrating that home ranges were not symmetrical but had complex and irregular 2-dimensional topography. The areas of highest usage (core areas) were not always central to the total area used (Fig. 5). The data were used to define core areas, which were those 20×20m bins in which fish spent greater than 2% of their time. It was also common for fish to have two or more separate core areas (Figs. 6 & 7). Utilization of space was seen to vary between individuals (Table 3). Some fish spent a high proportion of time in one small area (Fig. 5) while space usage in other fish was more evenly dispersed (Figs. 8 & 9). Fish 54Khz was found to reside for more than 30% of both the February and May monitoring periods in the same 20×20m bin (Figs. 5 & 10). Conversely, in May other fish did not even revisit some of the areas they had used most intensively in February (Figs. 6 & 8). While the central home range areas of most fish moved less than approximately 40 m, the core area of fish 60Khz moved ~300m between February and May (Figs. 11 & 12).

### Seasonality

The degree of site fidelity expressed by each fish was found to vary between February and May (Table 3), although there was no consistent trend. During this period fish 54Khz increased the percentage of time it resided in its core areas from 64.2 to 81.6%. Conversely fish 50 & 60Khz both began to utilize more than one core area and decreased the time spent in these areas by 42.9 and 30.5% respectively (Table 3).

**Table 3:** Space utilization characteristics for six *P. auratus* monitored in Goat Island Bay. Column headers are defined as: (1) Maximum diameter is the greatest distance between any two positional fixes for each fish, (2) maximum residency is the highest percentage of time each fish spent within one 20×20m bin, (3) size of core areas is calculated from the number of adjacent 400m<sup>2</sup> bins with greater than 2% residency (if two separate areas with greater than 2% residency exist then the size of each core area is listed) and (4) percentage residency within core areas is the total percentage of time each fish spent within each respective core area as defined in (3).

		(1) Max. Diameter (m)	(2) Max. Residency (%)	(3) Size of Core Areas (m <sup>2</sup> )	(4) Residency (%) within Core Areas
<b>50Khz</b>	February	380	12.2	300	60.5
	May	380	3.7	80 & 40	11.4 & 6.2
<b>54Khz</b>	February	500	30.2	140 & 60	55.2 & 9
	May	400	30.5	160 & 20	78.6 & 3
<b>57Khz</b>	February	400			
	May	360	19.8	180 & 20	44 & 12.7
<b>60Khz</b>	February	520	34.8	120	72.9
	May	460	7.4	220 & 80	37 & 11.4
<b>63Khz</b>	February	320			
	May	300	17.4	260	75.7
<b>78Khz</b>	February				
	May	240	12.3	180 & 40 & 20	56.2 & 6 & 2.9

During late February and early March, each of the five tagged fish made excursions of up to 300 m from their core area to North Reef, on at least one occasion. This is represented in the data by a concentration of fixes in the bottom right of the graphs in Fig. 3 that are not present in the graphs of Fig. 4. Such excursions contributed up to 16.7% of the February monitoring period for Fish 54 KHz.

**Table 4:** Probabilities of individual fish being found at varying distances from their respective core areas. The tagged fish were fish 60 Khz and fish 54 Khz.

	<b>60Khz (May)</b>	<b>54Khz (May)</b>
<b>Core area size</b>	200m <sup>2</sup>	160m <sup>2</sup>
<b>Outside of core area</b>	0.63	0.214
<b>&gt;60 m from core area</b>	0.415	0.078
<b>&gt;120 m from core area</b>	0.31	0.013
<b>&gt; 180 m from core area</b>	0.14	-
<b>&gt; 240 m from core area</b>	0.019	-

The movement information obtained from the tags was used to estimate the proportion of time that a fish spends at varying distances from its core areas. As noted above, the movements of individual fish varied substantially. The most active fish spent over 40% of its time at distances 60m or greater from the centre of its core area, while the least active fish spent only 7.8% of its time more than 60m from the centre of its core area (Table 3). Fish 54Khz was highly resident and would only be expected to move more than 120 metres from its core area 1.3% of the time. However during the same period fish 60Khz was located at distances greater than 120 m from its core area on 31% of occasions.

## **Discussion**

This study represents the first detailed fine-scale and long term monitoring of individual movement patterns in *P. auratus*. Results show that all five surgically tagged snapper remained in areas of less than 400 m diameter for a very large percentage of the time. This is supported by re-sightings of ~50 individually tagged *P. auratus* remaining within an area of hundreds of metres of release (Willis *et al.* in press). This is not surprising as retaining a home range has energetic advantages that flow from familiarity and therefore efficient use of resources (Fretwell 1972, Kramer & Chapman 1999). Even

fish from highly mobile families such as the Carangidae have some highly site-attached species (Holland *et al.* 1996), demonstrating that, just because a species is capable of high mobility, it does not always express this behaviour.

### *Space utilisation patterns*

All of the fish tracked at the CROP Marine Reserve appeared to use some areas within their home range more extensively than others. This is logical, as some areas could provide better shelter or food than others. It remains unknown whether these core areas are where a fish resides when it is inactive (Lokkeborg *et al.* 2000) or whether a disproportionate amount of foraging and/or social interaction are occurring at these locations. This information could be crucial to understanding optimal reserve design and how marine reserves “work”. If a fish is inactive in its core area the majority of foraging, and therefore the highest likelihood of taking a bait, will be conducted while at the edges of its home range. The location of these core areas could therefore be either central or peripheral to important activities. Regardless of what resources are being utilised, they are unlikely to be distributed in a regular and symmetrical manner, therefore it is not unexpected that the distribution of fish ranges is asymmetrical and even polymodal. For example, during the February monitoring period excursions to the North Reef area resulted in a bipolar space utilization pattern as described above. Fish spent up to 16% of time at this location, not including the time taken to travel to and from the reef. The fact that all *P. auratus* with surgically implanted transmitters made such excursions from their core areas only in February may be of unique importance.

Structural complexity is known to increase the abundance of prey items (Fretwell 1972) and North Reef rises from 25 m depth to within 2 m of the surface. If bait-fish school around North Reef during summer then snapper may be attracted to that area in February. However February is also within the spawning period of snapper (Scott and Pankhurst 1992) and we speculate that excursions of tagged fish might be related to spawning behaviour. Seasonal spawning aggregations have been demonstrated for fish such as coral trout (Zeller 1998) and in the case of this species the boundaries of a marine park no-fishing area were redefined in order to include the spawning area. This

possibility needs to be confirmed for snapper, and potentially could be done by examining the small-scale distribution of snapper eggs during the spawning season (Zeldis 1998).

### *Behavioural variation*

It is our opinion that *P. auratus* express a full spectrum of mobility with some *P. auratus* moving hundreds of kilometres (Paul 1967) and others, as documented here, remaining resident in an area of only hundreds of metres in diameter. However even within the group of resident *P. auratus* used in this study, variability in movement patterns was observed. This is best illustrated by fish 54 and 60Khz (Table 3). Although each fish used a total area of around the same size, fish 54Khz resided in, or at close proximity to, its core area for a much higher proportion of time than fish 60Khz. If the core area of fish 54Khz was located 120 m from the reserve boundary, this fish would only be exposed to fishing pressure 1.3% of the time. In contrast, fish 60Khz, located at the same distance from the reserve boundary, could be vulnerable to fishing up to 31 % of the time. Fish 60 KHz's core area would have to be 240 metres from the reserve boundary before it was exposed to the same level of fishing pressure as fish 54 KHz. These figures assume that boundaries coincide with the direction of the fish's movement and are clearly simplistic in nature, but they do illustrate the potential implications of variations in individual fish behaviour on fishing effects.

An additional consideration to these simple variations in core area size is the potential for fish to shift their core area. A core area shift of 300 metres was documented for fish 60khz between February and May. If this occurred in the hypothetical near-boundary situation suggested above, the centre of the second core area would be located 60 m outside the reserve exposing this fish to fishing pressure for greater than 50% of the time. Fish 54Khz remained resident in exactly the same 20×20m bin and would still be exposed to fishing pressure 1.3% of the time in the aforementioned hypothetical situation. This behavioural difference, while only manifested on a scale of hundreds of metres, would make a large difference to the probability of mortality. Furthermore, the scale at which site fidelity and core area shifts operate could be expected to vary with location, depending on factors such as the availability of resources. In areas with low resources

and/or high levels of intraspecific competition it would be sensible to assume *P. auratus* could need to be wider ranging than observed here.

Variations in the degree of site fidelity expressed by each fish were also noted between the two sampling periods. While one fish increased its percentage residency within its core area in May, others were seen to use additional core areas and decrease the percentage residency within these areas. There is therefore no clear indication of seasonal change in movement pattern shown in the tagged fish.

#### *Extra-reserve excursions and their influence on protected snapper populations*

While there are clearly many variables influencing snapper behaviour that we are only now beginning to understand, we have used a series of three assumptions to generate some guidelines for designing the size and boundary configuration of marine reserves. The first assumption is to use the “worst case” scenario, and base these guidelines on the most active fish. This fish would require an area of radius 240m from the nearest boundary in order to ensure it did not spend more than 1% of its time in a fished area. One of the five fish (20%) displayed this behaviour. The second assumption was that there could be a linear translation in core area of up to 300m. Again, one of the five fish (20%) displayed this behaviour. Thirdly, since there would be only a 50% chance of a core area shifting towards, rather than away from, a boundary in any but the smallest reserve. We therefore calculate that the probability of a mobile fish spending more than 1% of its time outside an area of 540 m radius is 2% ( $0.2 \times 0.2 \times 0.5$ ). The remainder would be even less likely to move outside this area.

This is a tentative calculation, based on some very simplistic assumptions, however it does allow us to begin to attach numerical values to the distances that may be ecologically important in the context of snapper and marine reserves. Consequently, we tentatively recommend that offshore reserve boundaries be placed at a distance of no less than 540 m from the edge of any reef structures. Similarly, there is likely to be some effect of fishing on fish located adjacent to coastal boundaries of reserves if they have core areas less than 540 m from the boundary. These estimates are conservative in that

they use values from the most mobile fish. The observed pattern of lower fish abundance at the boundaries of the CROP reserve (Willis and Babcock 1998b) may be explained by limited movements of the magnitude we have described, however the effect seems to be occurring over distances greater than 540 m, and can in fact be seen in areas more than 1000 m from the coastal boundaries. If home range shifts do occur in response to density dependent factors it would be more probable that it would occur away from the centre of the reserve, where *P. auratus* abundances are highest (Willis *et al.* 2000). This would result in 'spill over' into the fishery adjacent to the reserve. While this can not be demonstrated here it could explain the observed pattern since the edge effect is much greater than 200m. One of the methods through which density dependent factors operate is intra-specific aggression (Fretwell 1972), such interactions between *P. auratus* have been frequently observed towards the centre of the CROP reserve (D. Parsons pers. obs.).

This report has made some general suggestions for marine reserve configuration based on simplistic scenarios of maximum levels of movement. A more realistic set of suggestions and an analysis of the implications of marine reserve protection for snapper populations both within and outside of reserves can now, for the first time, be contemplated, based in part on the data we have collected. Such an analysis will need to be based on spatially explicit numerical models of snapper populations, rather than simplistic assumptions such as we have used, and will be the next major step forward in this process.

## **Conclusions**

The degree of site fidelity expressed by *P. auratus* in this study is higher than documented by any other study. However individual variation was also noted as being a major factor. While fishing pressure was demonstrated to possibly have an effect on *P. auratus* hundreds of metres inside the reserve, other *P. auratus* could reside close to the reserve boundary with minimal chance of mortality. The pattern of usage does not always appear to be uniform, can vary seasonally and fish can heavily utilize separate areas. During February some fish spent up to 16% of their time outside of their core areas at a location only frequented during this period.



With a seasonal emigration of around 50% of *P. auratus* from inshore reefs (Willis & Babcock 1998b, Willis & Denny 2000) it appears that some fish are more mobile than others. If a fish species has more than one level of mobility, inside a reserve the most highly resident fish will be favoured (Attwood & Bennett 1994). For this reason, it is essential that a central area containing the correct habitats, where resident fish are removed from fishing pressure, be incorporated into reserve design.

## **Recommendations**

1. There is a need to compare movements of fish in central, peripheral and non-reserve locations. Why are boundary edge-effects on fish density detectable at least 1km inside the CROP reserve, when core areas in the central reserve have a maximum radius of 200m?
2. The reason for core area excursions should be further studied to determine whether they are feeding or spawning related. Such excursions are a potential explanation for edge effects.
3. Tagging of larger numbers of fish on a more extensive spatial scale (10's of km) is needed to determine the timing and extent of movements and potential return of *P. auratus* that disappear from coastal reefs over winter. The effectiveness of marine reserves in relation to snapper of a mobile nature can only be determined by expansive tracking.
4. Numerical modeling of fish movements in relation to marine reserves should be undertaken in order to assess the implications of snapper movement patterns on the effectiveness of reserves, optimal reserve size, and 'spillover'.

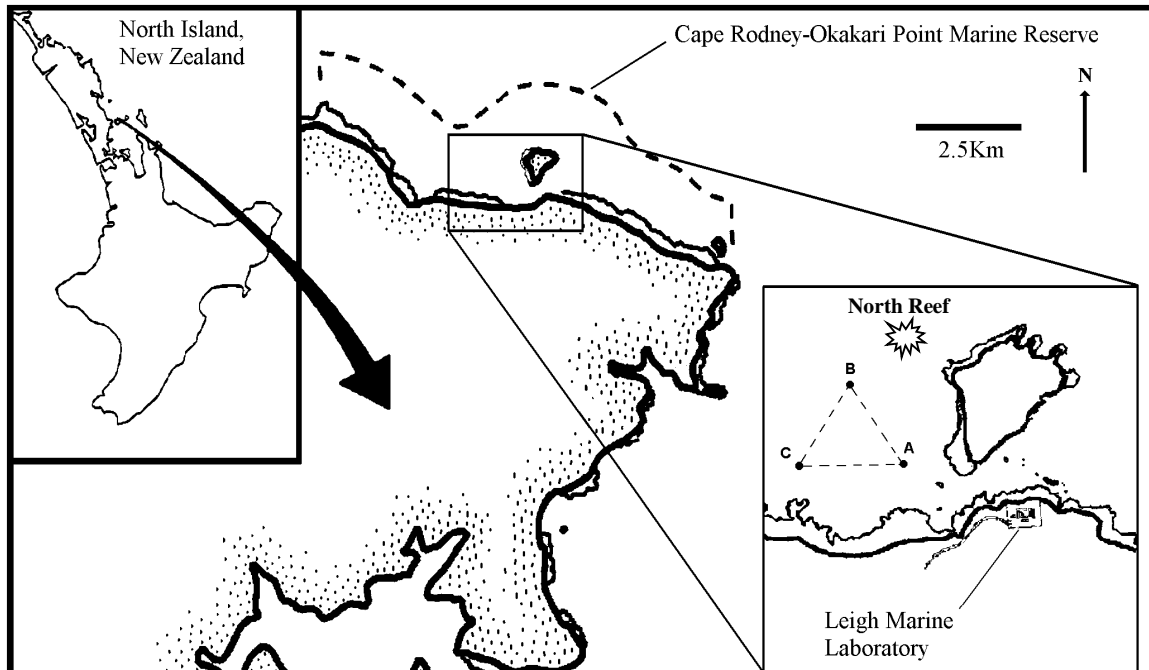
## **Acknowledgements**

We would like to thank Dalhousie University for assistance through the expertise of Dr Ron O'Dor and Jill Aitken, Port Lincoln University, South Australia, for provision of equipment and Dr Graham Allen for help with data analysis. This report would not have been possible without the voluntary assistance provided by Phil Ross, Bryna Flaim, Schannel van Dijken, Phillipa Stokes and Brenda Muller. Finally I would like to thank David Feary for his endless hours of unrewarded assistance.

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**Fig. 1:** Map of the CROP Reserve showing the location of the buoy array. Sono-buoys A, B & C are positioned approximately 300m apart.

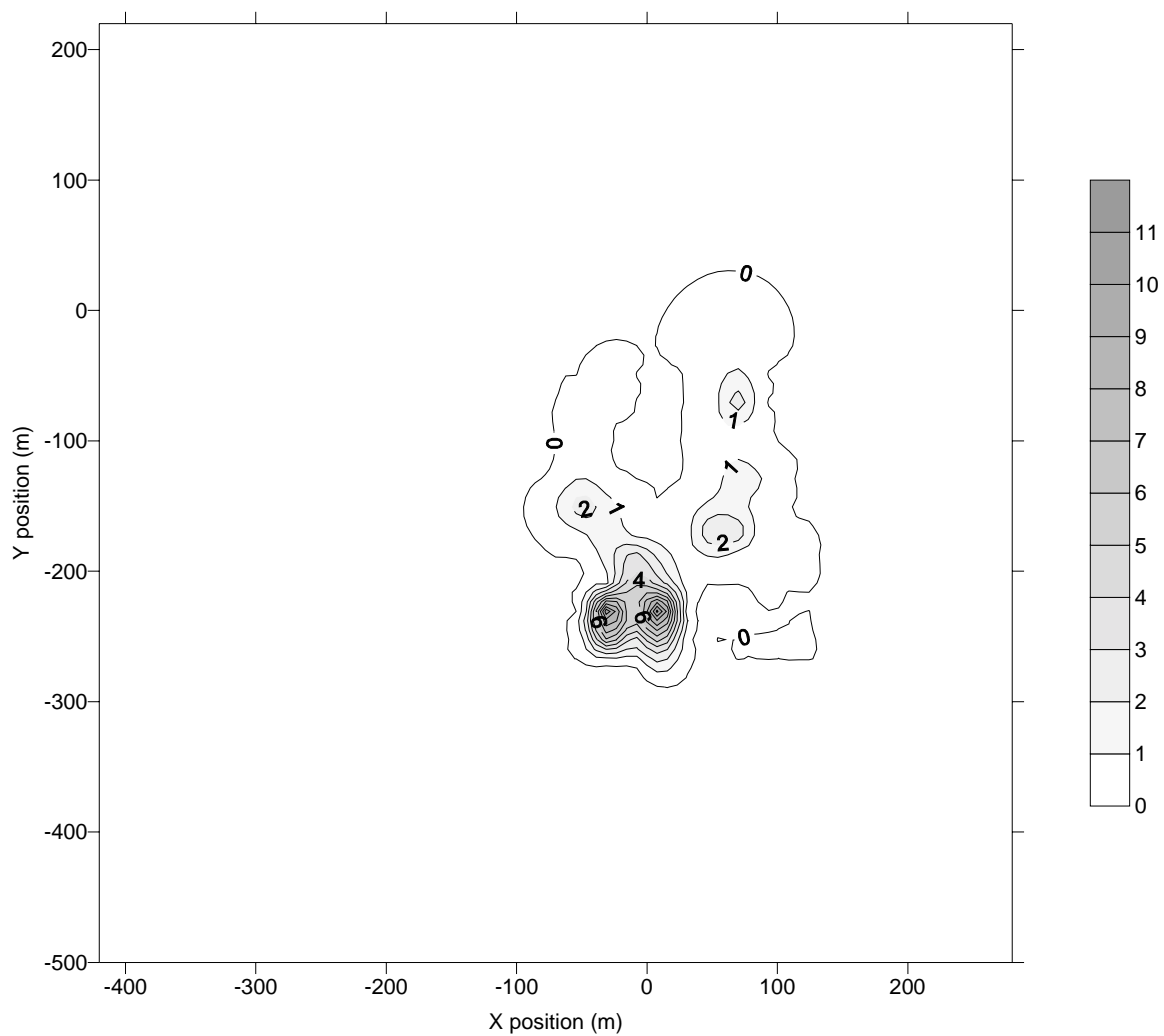
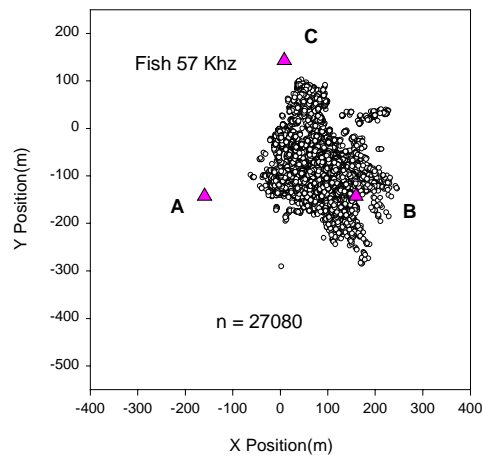
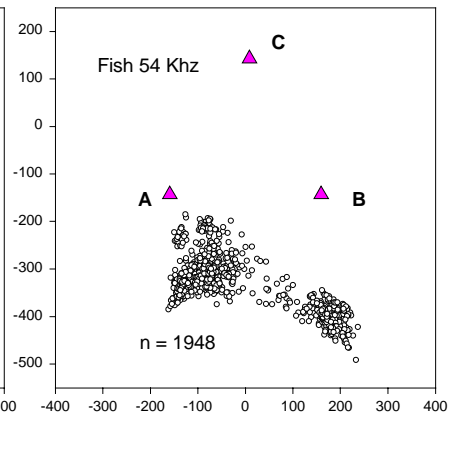
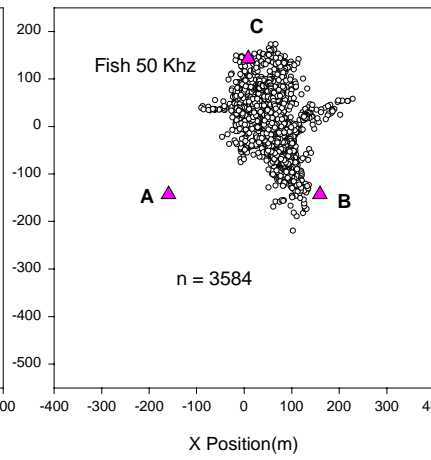
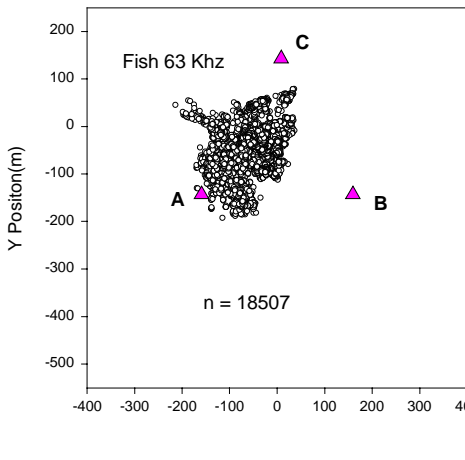
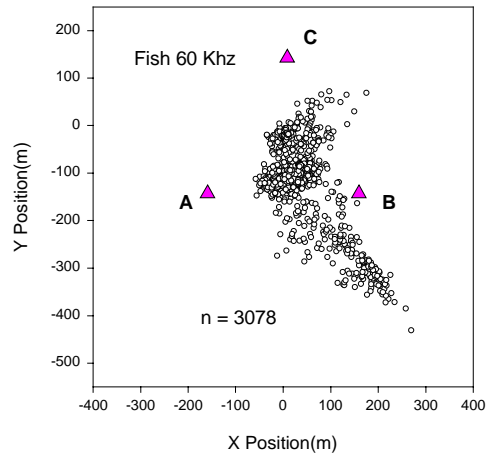


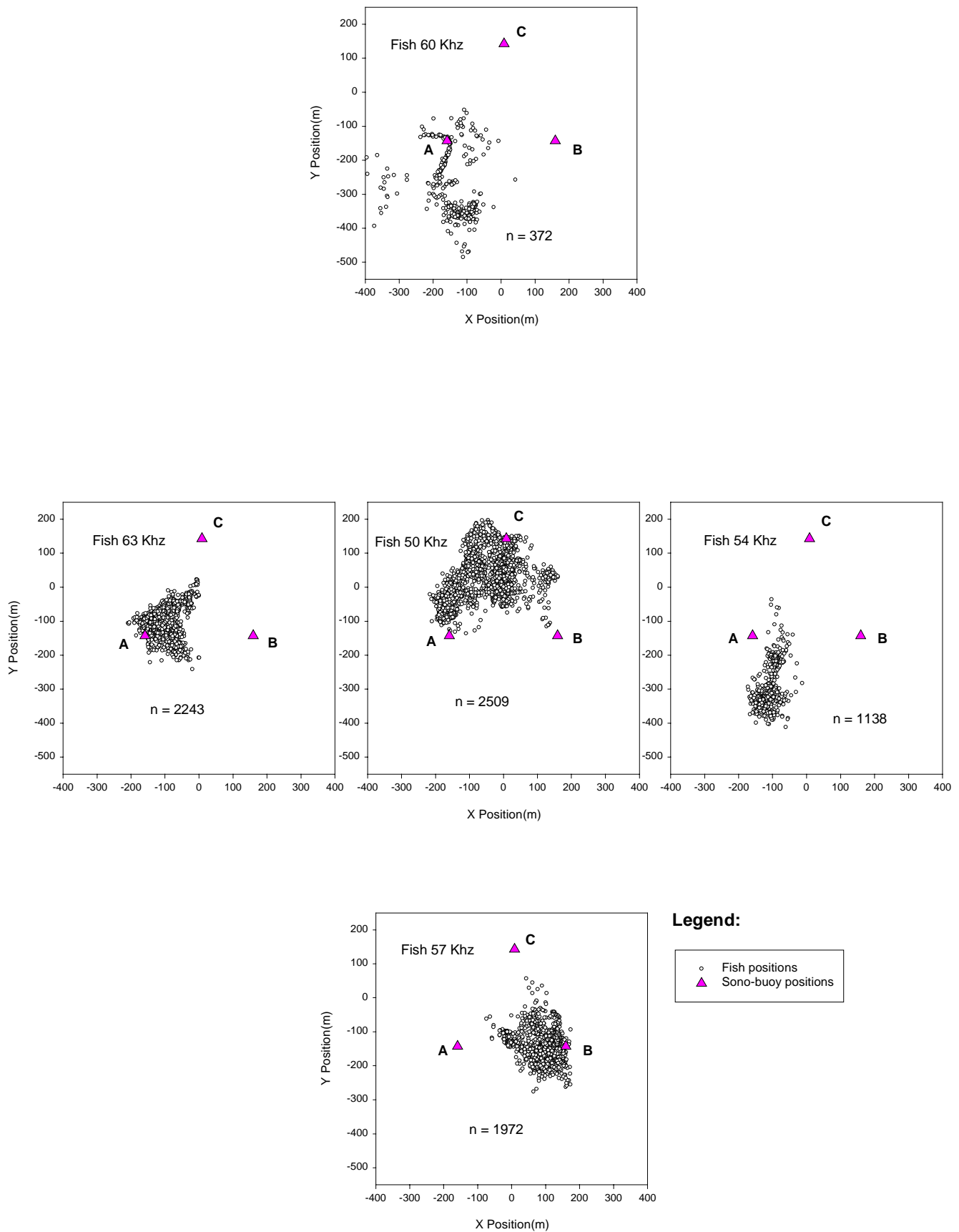
Fig. 2 : Percentage residency time of fish 78Khz (voluntary ingested transmitter) for the May sampling period (total tracking time = 3.2107).  
N.B. These contour plots use a grey scale of percentage residency time, where the darker tones represent a higher percentage residency and each contour represents a 1% difference in residency.



**Legend:**

- Fish positions
- ▲ Sono-buoy positions

**Fig. 3:** Positional fixes of five individually tagged snapper from the 10th to the 17th of February 2000 (NB: individual fish defined by the frequency of their transmitter).



**Fig. 4:** Positional fixes of five individually tagged snapper from the 20th to the 29th of May 2000 (NB: Individual fish are defined by the frequency of their transmitter).



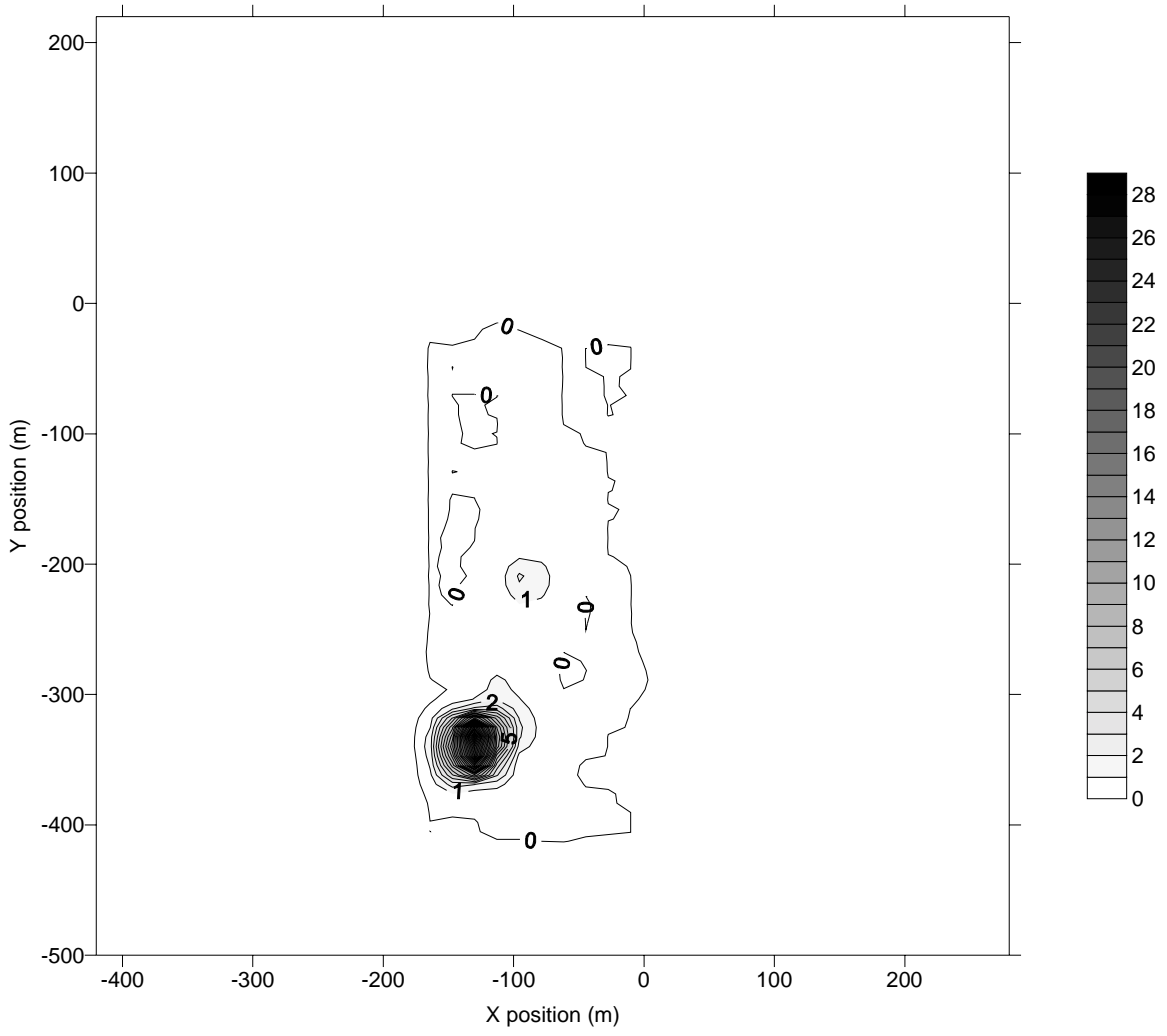


Fig. 5 : Percentage residency of fish 54Khz for the May monitoring period (total tracking time = 5.4622 days)

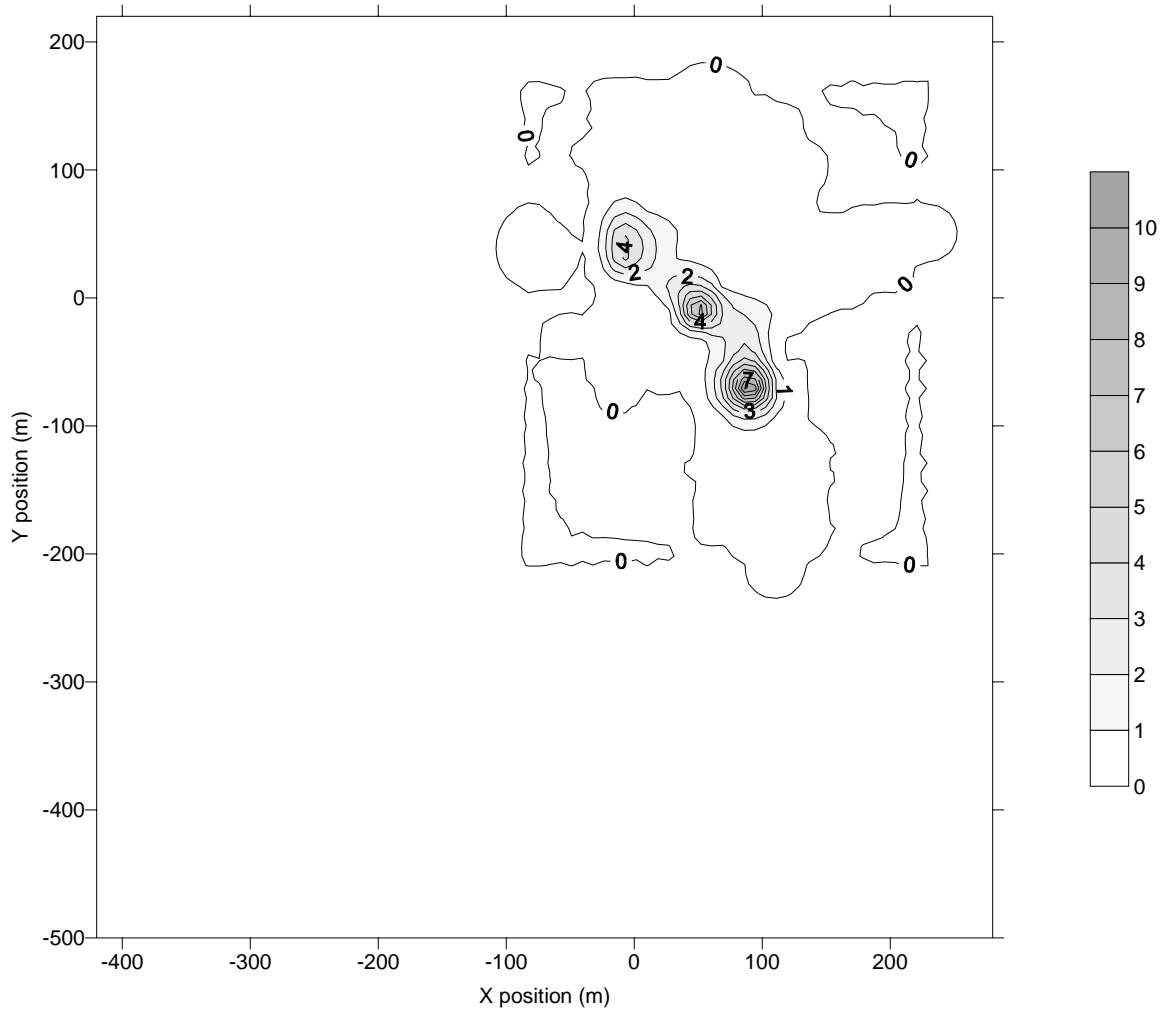


Fig. 6 : Percentage residency time of fish 50kHz for the February monitoring period (total tracking time = 7.7172 days)

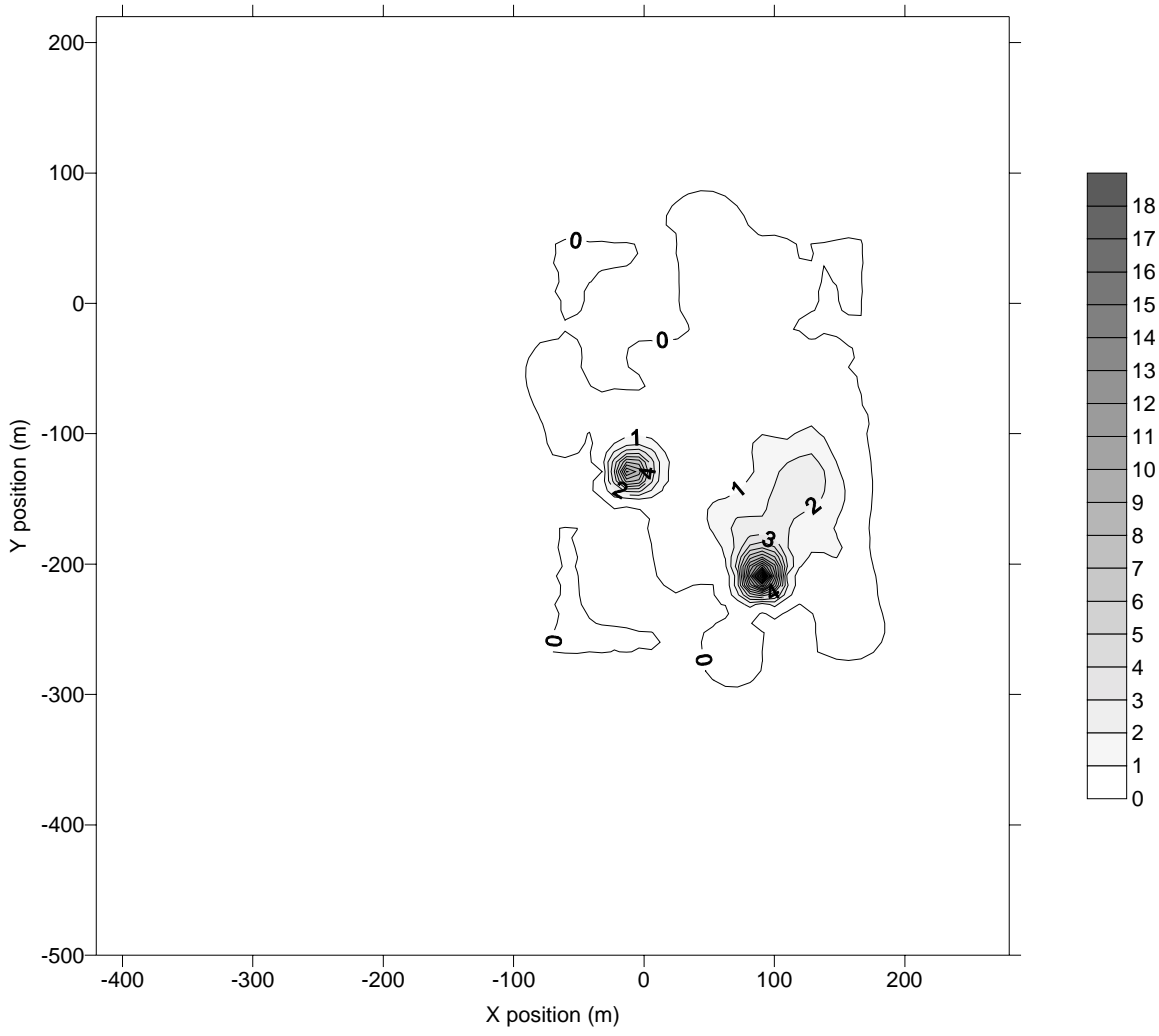


Fig. 7 : Percentage residency time for fish 57Khz in the May sampling period (total tracking time = 6.8241 days)

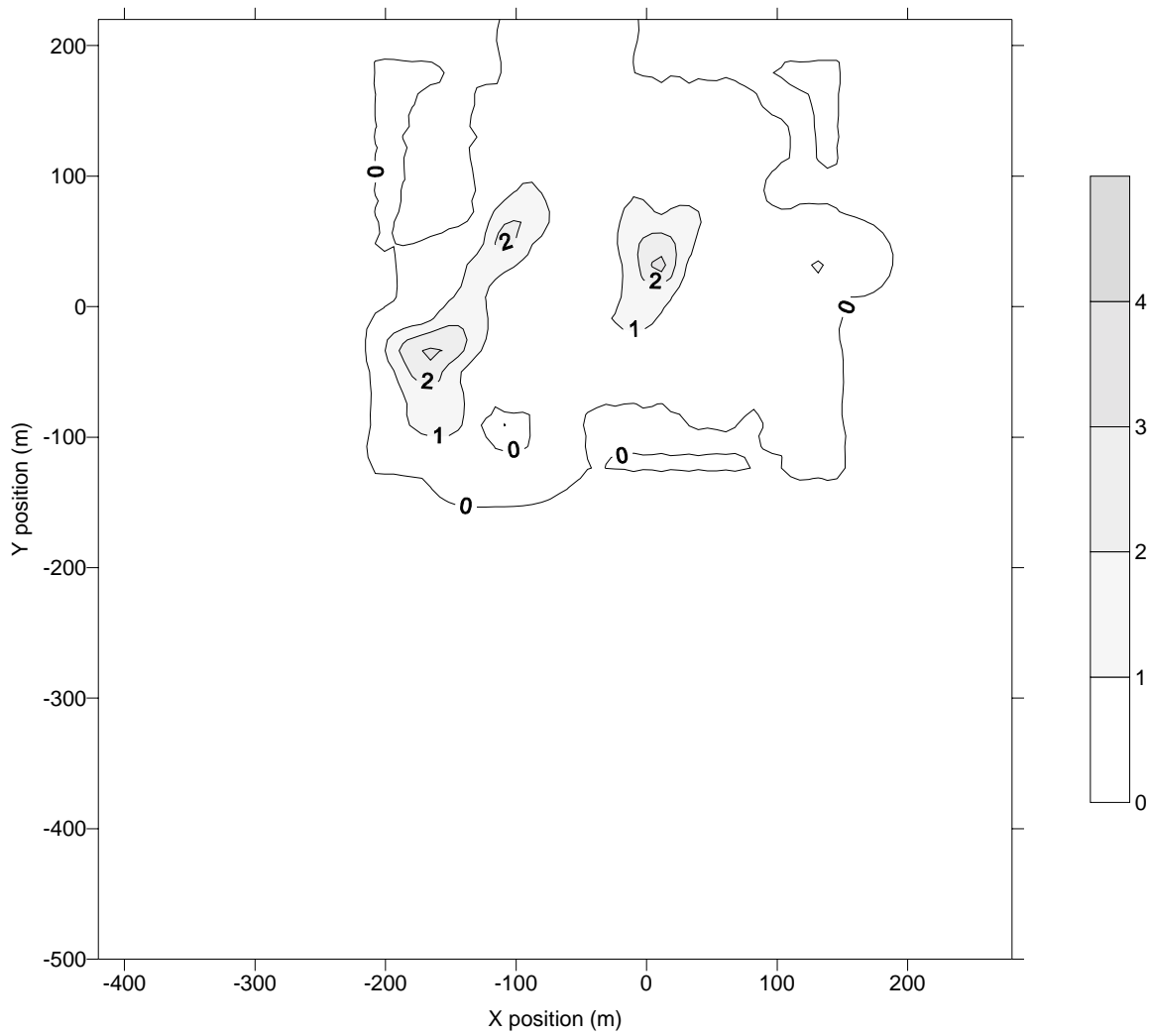


Fig. 8 : Percentage residency time of fish 50Khz for the May monitoring period (total tracking time = 6.9682)

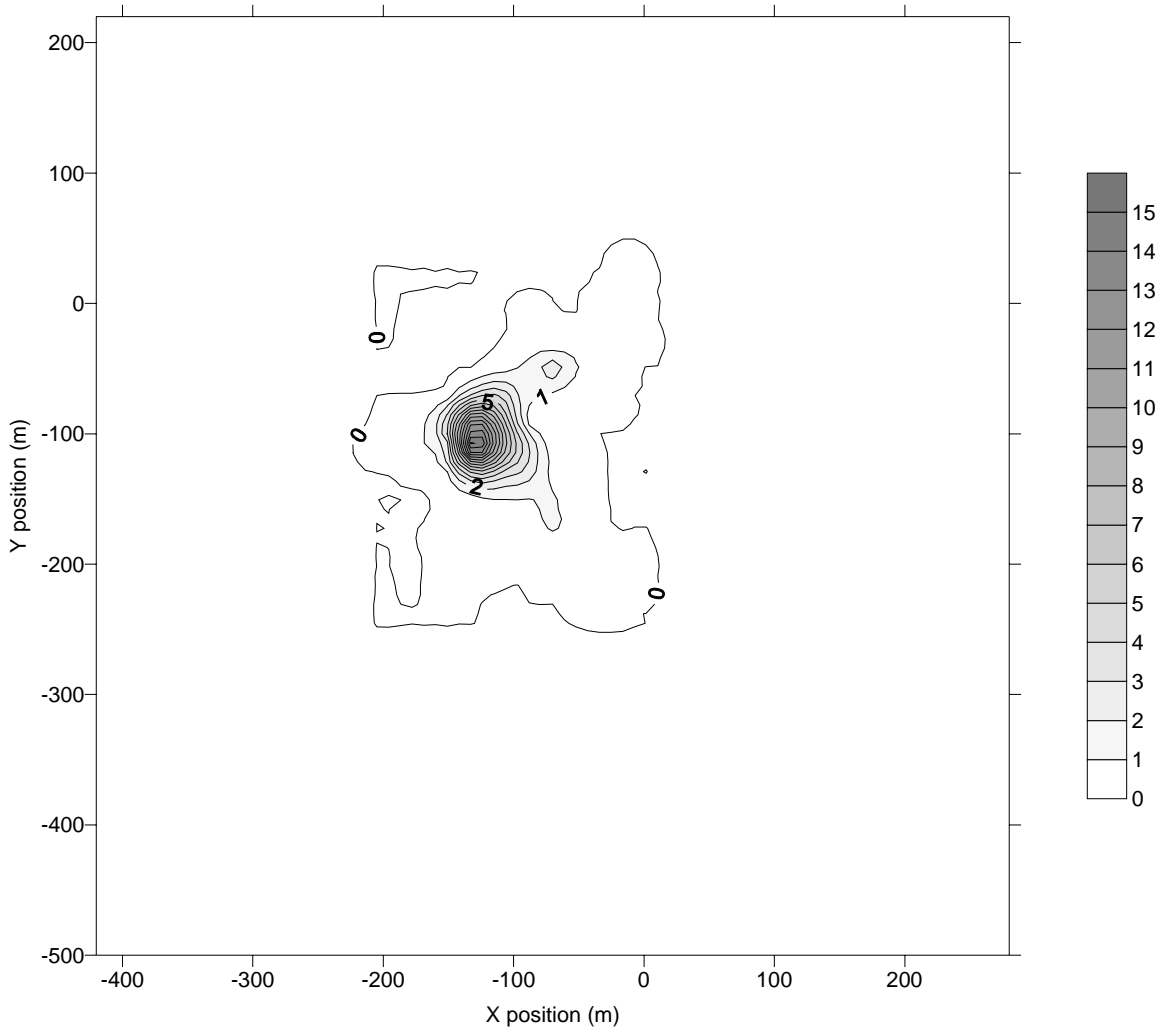


Fig. 9 : Percentage residency time of fish 63Khz for the May monitoring period (total tracking time = 6.8055 days)

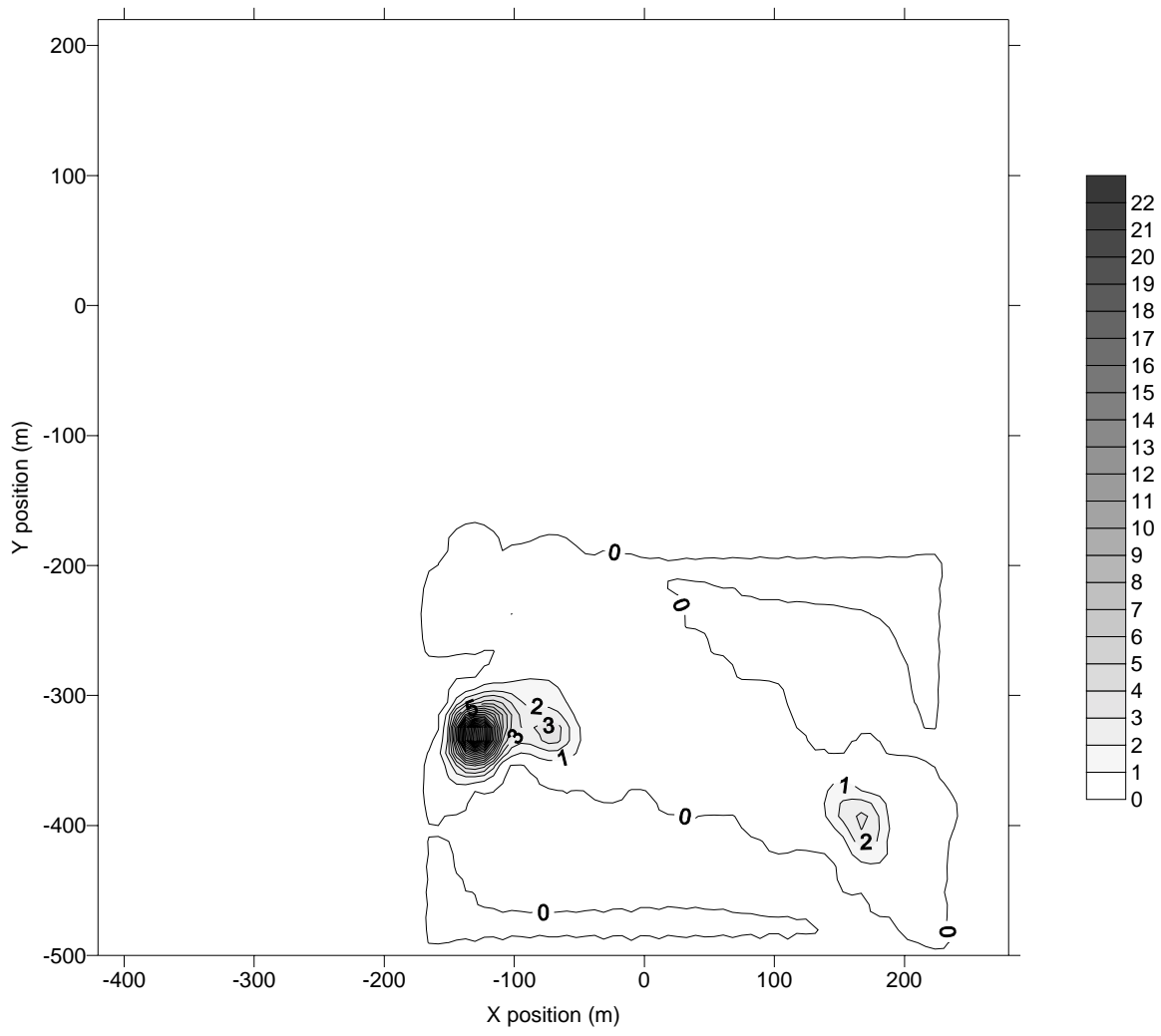


Fig. 10 : Percentage residency time of fish 54Khz for the February monitoring period (total tracking time = 7.7172)

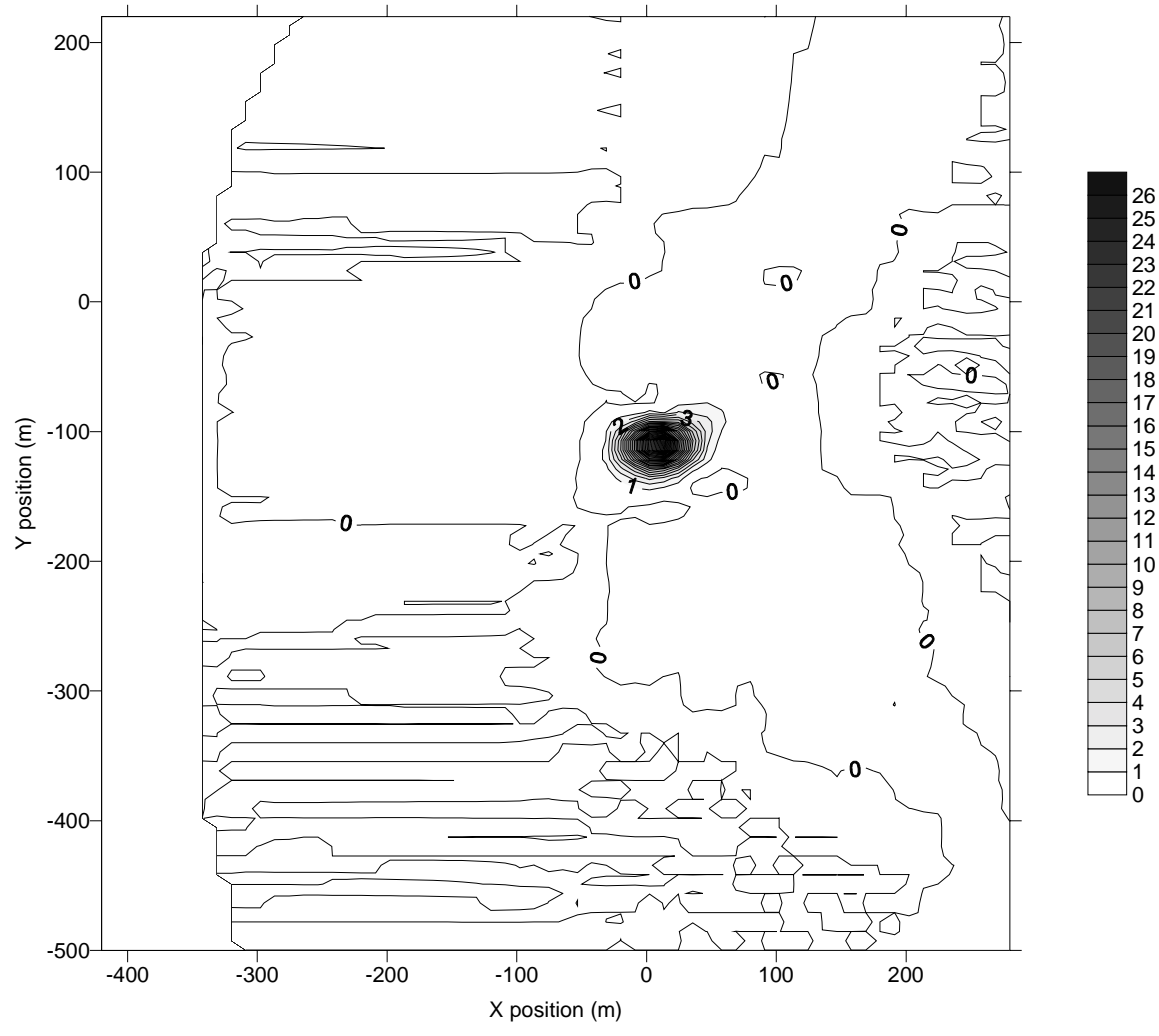


Fig. 11 : Percentage residency time of fish 60Khz for the February monitoring period (total tracking time = 7.5593 days)

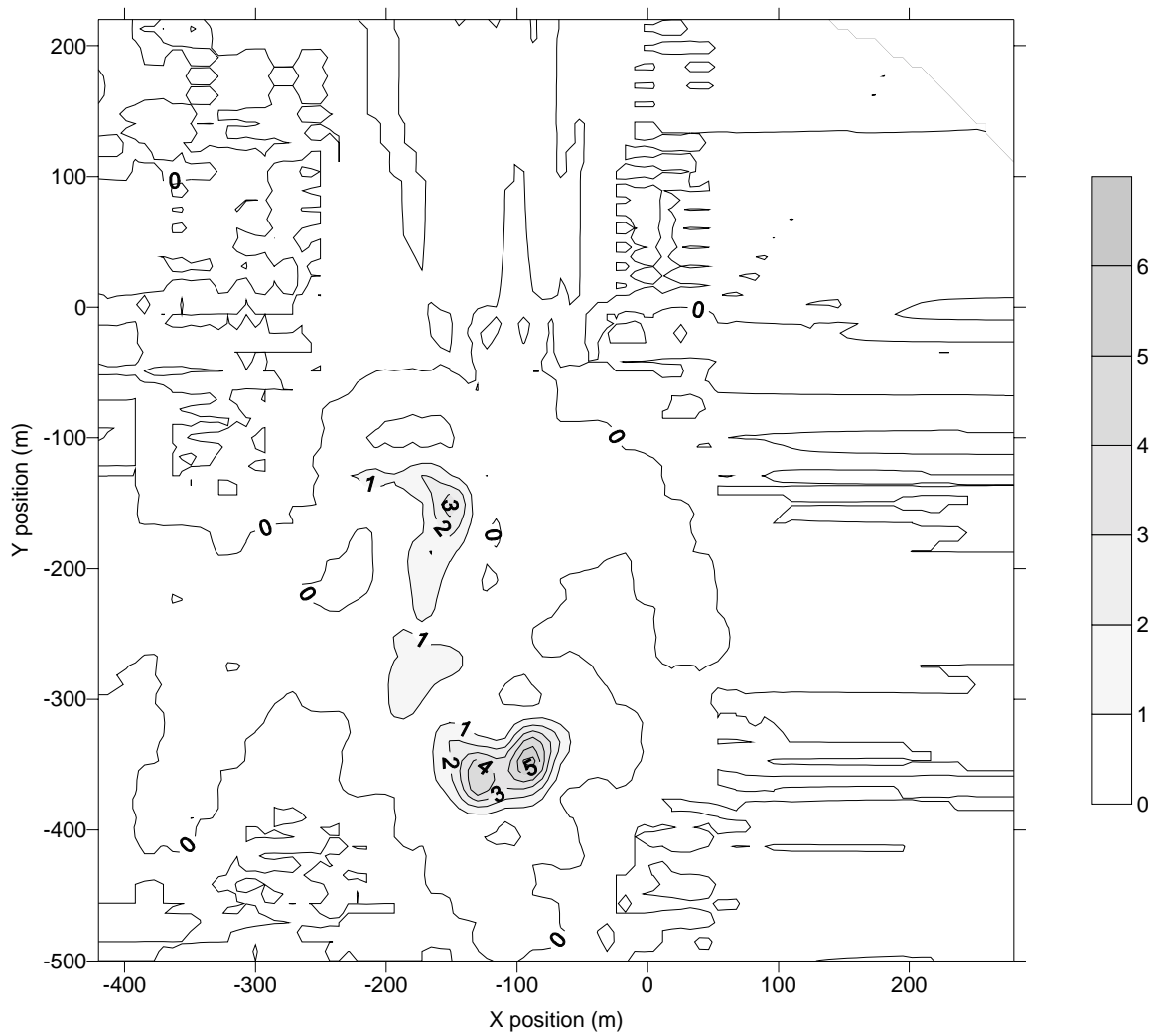


Fig. 12: Percentage residency time of fish 60Khz for the May monitoring period (total tracking time = 2.6754 days)