THE EFFECT OF TEMPERATURE AND TURBIDITY ON SPAWNING CHOKKA SQUID, *LOLIGO REYNAUDII*, IN EASTERN CAPE WATERS

By

Nicola Jean Downey

Submitted in fulfilment of the requirements for the degree
of Masters in the Faculty of Science at the Nelson Mandela
Metropolitan University

April 2009

Supervisor: Prof. D. Baird
Co-Supervisors: M.J. Roberts
Dr. D. Winter

DECLARATION BY STUDENT

FULL NAME: Nicola Jean Downey

STUDENT NUMBER: 202308790

QUALIFICATION: Magister Scientiae

DECLARATION:

In accordance with Rule G4.6.3, I hereby declare that the above-mentioned treatise/ dissertation/ thesis is my own work and that it has not previously been submitted for assessment to another University or for another qualification.

SIGNATURE: N J Downey

DATE: 1 April 2009

Table of Contents

List of Figures

List of Tables

Abstract

Several studies suggest the environment influences chokka squid catches which are mostly based on the successful formation of inshore spawning aggregations. None of the evidence, however, is direct observation. Acoustic telemetry offers a means to determine the response of spawners to changes in the environment and insight into the behaviour of spawning squid. A hexagonal array of VR2 receivers deployed 500 m apart was deemed to be ideal to monitor the movement patterns of squid on the spawning sites. In isothermic conditions, an area up to 1.28 km^2 could be monitored as there was an approximate 50 m overlap in individual VR2 receiver range. In thermocline conditions however, "acoustic dead zones" as wide as 350 m may have existed between VR2 receivers, limiting the performance of this configuration. Similarly benthic turbidity events would also decrease detection range and limit performance. A hexagonal array of VR2 receivers was moored in Kromme Bay on and around active spawning aggregations during the squid fishery closed seasons of November 2003, 2004, 2005 and 2006. Squid were caught on jigs and tagged with V9 acoustic pressure telemetry transmitters. A total of 45 animals were tagged. Presence-absence analysis identified three general behaviours: (1) arrival at dawn and departure after dusk, (2) a continuous and uninterrupted presence for a number of days and (3) presence interrupted by frequent but short periods of absence. Overall, the data suggests frequent migrations between spawning aggregations and offshore feeding grounds. The pressure sensor data showed both males and females stayed persistently near the seabed during the day, but at night, this pattern was broken with common activity higher up in the water column. The squid did not remain exclusively in the water column and regularly made excursions to the seabed. CTD and temperature data indicated the intrusion of a cold bottom layer due to upwelling at the monitored spawning sites on a number of occasions. The formation of spawning aggregations appears to be triggered by upwelling events and spawning behaviour, once initiated, disrupted by upwelling events with a rapid onset, possibly due to an inability to adapt physiologically over such a short time period.

List of Abbreviations and Symbols

s.d.	standard deviation
M#	tagged male squid (# indicates unique ID number)
SM#	tagged sneaker male (# indicates unique ID number)
F#	tagged female squid (# indicates unique ID number)
OBS-3A	suspended solids and turbidity monitor (previously D & A Instrument Company, currently Campbell Scientific)
UTR	Star-oddi Starmon mini underwater temperature recorder
CTD	portable conductivity-temperature-density recorder (Seabird 19 Plus)
NTU	nephlometric turbidity unit
ODV	Ocean Data View – Computer programme used to generate gridded horizontal plots
ADAS	ADCP Data Analysis Software – Computer programme used to generate wind stick vector plots
Acoustic transmitter	a tag that emits acoustic signals
Receiver	instrument that records signals from acoustic transmitters (VR2 receiver – passive tracking; VR100 – active tracking)
Passive tracking	monitoring movement of acoustically tagged animals using stationary receivers
Active tracking	monitoring movement of acoustically tagged animals using a VR100 and a boat. The hydrophone of the VR100 is placed in the water and the strength and direction of detected signals used to manually track acoustically tagged animals
Acoustic array	group of stationary receivers used for passively tracking acoustically tagged animals

Acknowledgements

This work has been supported and funded by the Nelson Mandela Metropolitan University, the National Research Foundation, Marine and Coastal Management and the South African Squid Management Industrial Association. I wish to thank these organizations for the opportunity to do this research.

To my supervisors Prof. Dan Baird, Michael John Roberts and Dr. Deo Winter: Thank you for all the input and support, the many hours you have each dedicated to this work and your guidance throughout.

To Dale Webber, Warwick Sauer and Malcolm Smale: Thank you for introducing me to the exciting world of acoustic telemetry and for all the in-field training and assistance. I have enjoyed every moment of it!

To the Bayworld Centre for Research and Education team Larvika Singh, Marcel van den Berg, Tamaryn Morris, Rick Harding, Niel Engelbrecht, Bradley Blows, Fiona Duncan, Lisa Hancke and Lloyd Duncan: Thank you for all the support in the field, the hours you spent on and in the (often rough) water and for the MANY, MANY laughs. This project would have been impossible without you.

And last but by no means least, to my parents Jean and Garth Downey: Thank you for your love and understanding and for always believing in me.

CHAPTER 1

General Introduction

Initially chokka squid, *Loligo reynaudii* (previously known as *Loligo vulgaris reynaudii*[I]), was targeted by line-fishermen for use as bait. By-catch from trawlers was also packed for bait (Augustyn 1989). With calamari becoming a popular restaurant dish in the late 1970's (Augustyn 1989), a fishery specifically targeting the chokka squid began to develop. By 1984 and 1985, the price of chokka squid on the international market began increasing (Augustyn 1989) and an increased number of boat owners and fishermen invested in the South African squid fishery (Augustyn 1989). A handline jigging fishery consisting of small-boat owners and entrepreneurs was established in 1985 (Augustyn and Roel 1998). The chokka squid fishery has since developed into the most important cephalopod fishery in South Africa (Augustyn 1986).

The Japanese, Spanish and Italian squid markets are the three major markets in the international squid trade (Josupeit 2005). The bulk of South African *L. reynaudii* is exported to Spain and Italy. Regarding *Loligo* spp. specifically, South Africa is the third largest supplier to both Spain (Table I) and Italy (Table II). As *L. reynaudii* is sold as "fresh" produce, it is second highest in value per kilogram on the Spanish market (Table I) and the highest in value per kilogram on the Italian market (Table II). When considering the contribution of South African chokka squid to total annual imports of squid to Spain and Italy, South Africa is not a major contributor. The importance of the South African squid fishery however, lies in its contribution to the local economy of the Eastern Cape, bringing in foreign revenue to the value of about R100 million per annum (Cochrane *et al.* 1997) and creating jobs for approximately 6600 fishers. These fishermen rely solely on the income generated from the squid fishery.

[I] Vecchione, M. 2008. Tree of Life Web Project. http://tolweb.org/Loligo/19858/2008.03.04

Table I: *Loligo* spp. imports to Spain for the years 2003 and 2004, value of imports in Euros and Euro/kg for the various *Loligo* spp.

Loligo spp. Imports to Spain						
	Tons		**Euro**		**Euro/kg**	
Country	**2003**	**2004**	**2003**	**2004**	**2003**	**2004**
Falkland/Malvinas	41 711	27 598	85 369 000	69 128 000	2.05	2.5
India	11 607	16 389	25 704 000	29 574 000	2.21	1.8
South Africa	4 285	6 295	20 071 000	27 935 000	4.68	4.44
China	3 670	4 933	5 842 000	9 316 000	1.59	1.89
Morocco	2 480	1 258	17 555 000	10 502 000	7.08	8.35
Korea Rep.	1 223	402	3 186 000	1 004 000	2.61	2.5
Others	20 050	22 694	45 269 000	54 028 000	2.26	2.38
Total	85 026	79 569	202 996 000	201 487 000		

Table II: *Loligo* spp. imports to Italy for the years 2003 and 2004, value of imports in Euros and Euro/kg for the various *Loligo* spp.

Loligo spp. Imports to Italy						
	Tons		**Euro**		**Euro/kg**	
Country	**2003**	**2004**	**2003**	**2004**	**2003**	**2004**
Spain	19 001	15 604	47 361 000	42 798 000	2.49	2.74
Thailand Rep.	17 824	19 524	41 870 000	46 713 000	2.35	2.39
South Africa	5 384	6 291	25 090 000	27 045 000	4.66	4.3
USA	1 084	1 660	2 360 000	3 290 000	2.18	1.98
Korea Rep.	968	1 351	2 826 000	4 152 000	2.92	3.07
Others	18 758	19 043	44 426 000	45 245 000	2.37	2.38
Total	63 019	63 473	163 933 000	169 243 000		

When examining chokka squid catch statistics, fluctuations in monthly (Fig. 1a) and annual (Fig. 1b) catches are immediately apparent. An average of 6 000 tons are caught per year but annual catches can fluctuate between 2 500 and 10 000 tons. The degree of this fluctuation is evident in Fig. 2, where deviation from the monthly average has been plotted. Annual catches varying as much as 7 500 tons combined with the unpredictable nature of these fluctuations has severe financial and socio-economic consequences. During periods of prolonged good catches, it is tempting and sometimes necessary for those involved in the industry to build capacity. This however further increases the risk factor during periods of poor catches. A second and far reaching consequence is the effect on the ~6600 fishermen and their families. Squid fishermen do not receive a set monthly income, but instead are paid in cash on a commission basis per fishing trip. Income earned is therefore entirely reliant on the amount of squid caught by each fisher per trip. During periods of low or no catches, the fishermen and there dependents suffer. A further consequence of the no squid, no pay system is an escalation in crime rates in these communities and surrounding areas when catches are poor.

Cephalopod species are sensitive to environmental fluctuations (Pierce *et al*. 2008) and a number of studies have shown a relationship to exist between the distribution and abundance of squid and the environment (*L. reynaudii*-(Augustyn 1990; Augustyn 1991; Roberts and Sauer 1994; Sauer et al. 1991), *L. forbesi*-(Pierce *et al*. 1998; Waluda and Pierce 1998), *L. vulgaris vulgaris*-(Lefkaditou *et al*. 1998; Lloret *et al*. 2001; Moreno *et al*. 2007; Valavanis *et al*. 2004; Valavanis *et al*. 2005; Waluda and Pierce 1998), *Todaropsis eblanae*-(Hastie *et al*. 1994; Rasero 1994) *Illex argentinus*-(Bakun and Csirke 1998; Sacau *et al*. 2005; Waluda *et al*. 2001; Waluda *et al*. 2008), *I. coindetti*-(Cuccu *et al*. 2008; Jereb *et al*. 2001; Jereb *et al*. 2005; Valavanis *et al*. 2004; Valavanis *et al*. 2005). These fluctuations in abundance lead to unreliable catches. The need to manage and forecast squid stocks have been the two major driving forces behind squid research in South Africa for the past 30 years.

The general aims of this thesis are to determine the influence of the environment on aggregations of spawning squid and hence the influence on squid catches. The following chapter highlights past research projects with the aim of understanding the spawning behaviour of chokka squid and effect of various environmental conditions on these spawning aggregations.

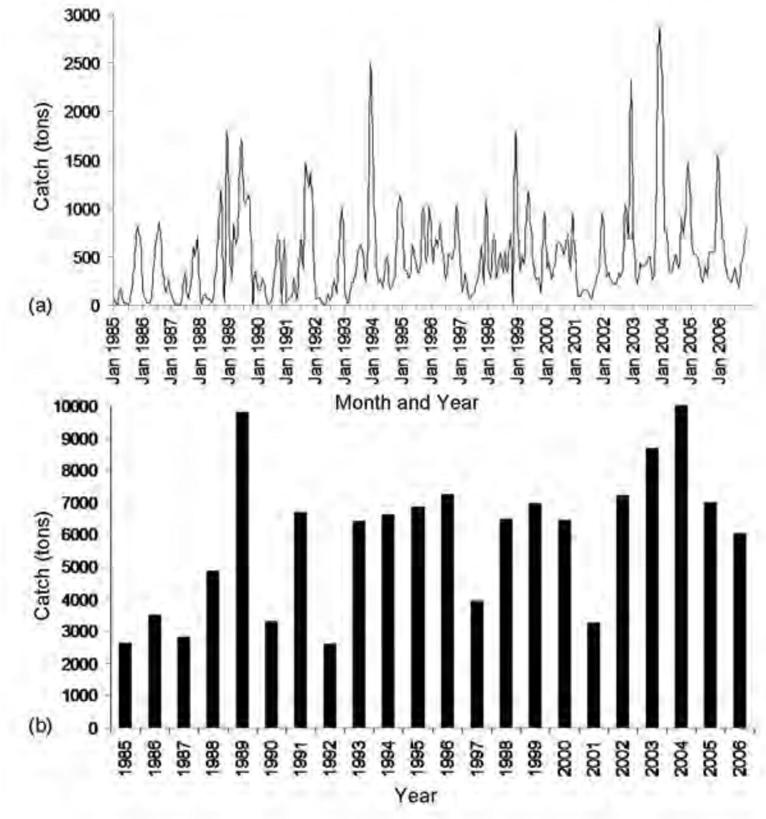


Figure 1: South African chokka squid *Loligo reynaudii* jig catch statistics on a (a) monthly basis and an (b) annual basis for the years 1985 to 2006[II].

[II] Marine and Coastal Management 2008. Commercial Squid Fishery Catch Data.

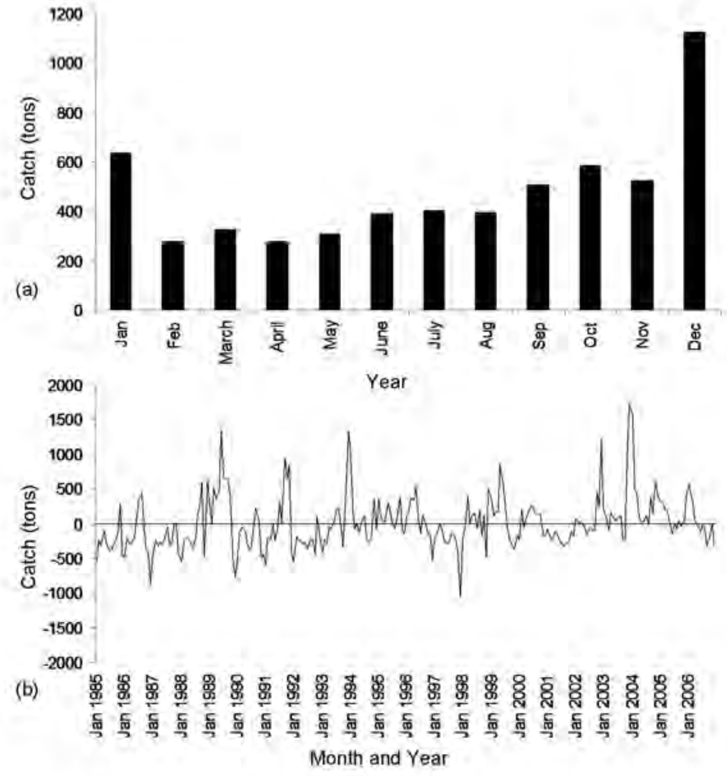


Figure 2: South African chokka squid *Loligo reynaudii* catch anomalies. (a) Average monthly catches calculated from monthly catch data for the years 1985 to 2006. (b) Deviation from the average monthly catch for the years 1985 to 2006[III].

[III] Marine and Coastal Management 2008. Commercial Squid Fishery Catch Data.

CHAPTER 2

Literature Review

The main spawning grounds of the chokka squid *Loligo reynaudii* occur on the South coast of South Africa between Plettenberg Bay in the west and Port Alfred in the east (Fig. 3) (Augustyn 1990). Squid form large spawning aggregations within this area, albeit sporadically (Augustyn 1990), throughout the year. The South African jig fishery; operating from two major ports, St Francis and Port Elizabeth (Fig. 3), specifically targets these spawning aggregations. As a result, catches are determined to a large extent by the successful formation of, size and quantity of these aggregations. In 1980, the Sea Fisheries Research Institute identified the reproductive behaviour and biology of the chokka squid to be a key research area. Consequently, a number of authors have investigated the spawning behaviour of *L. reynaudii*, namely Augustyn (1990;) de Wet (1995); Hanlon *et al*. (1994); Hanlon *et al*. (2002); Lipinski *et al*. (1998); Melo and Sauer (1999); O'Dor *et al*. (1996); Sauer *et al*. (1992); Sauer *et al*. (1993); Sauer *et al*. (1997); Sauer and Smale (1993); Smale *et al*. (2001). A summary of their findings follows.

Mature squid migrate from feeding grounds in the west (Augustyn 1990) to the south coast of South Africa. The squid remain in schools of separate sex (Sauer *et al*. 1992), probably gathering offshore (Smale *et al*. 2001) before moving inshore to form large spawning aggregations. The formation of these aggregations is thought to be largely dependent on the reproductive state of the ovaries of the female cohort (Roberts 1998). Precisely how the aggregations are formed i.e. which sex initiates the spawning process and what triggers the initial formation of such aggregations is as yet unknown. Observations on existing spawning sites; i.e. sites that already contain the characteristic footprint of the spawning process, egg beds (Roberts 1998), showed squid to arrive in the spawning area at dawn (Sauer *et al*. 1997). Large males then circled the egg bed, drawing in other males and female squid, and a spawning aggregation was formed (Sauer *et al*. 1997).

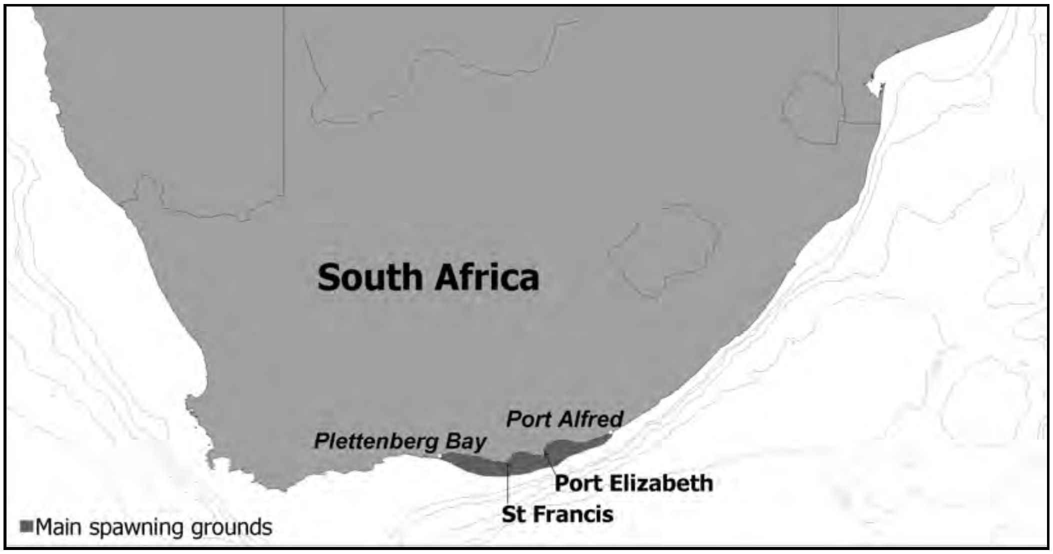


Figure 3: The main *Loligo reynaudii* spawning grounds on the south coast of South Africa between Plettenberg Bay in the West and Port Alfred in the East. Also indicated is Port Elizabeth and St Francis Bay (the study site for the research reported on in this dissertation).

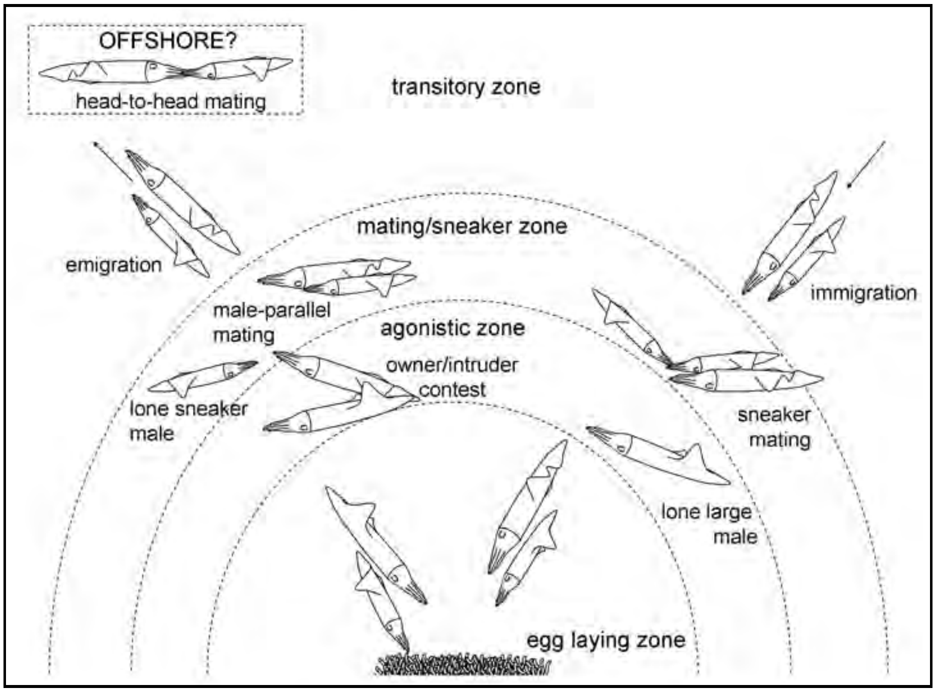


Figure 4: The general structure of a spawning aggregation for *Loligo reynaudii* (Hanlon *et al*. 2002).

Figure 4, taken directly from Hanlon *et al*. (2002), illustrates the general structure of the spawning aggregation. Pair formation occurs in the water column well above the egg beds (Sauer *et al*. 1992) in the mating/sneaker zone (Hanlon 1998; Hanlon *et al*. 2002). Once a pair has been formed the large consort male swims beneath the female, grasps her with his arms and transfers spermatophores, taken from within his own mantle cavity, into the females mantle cavity and places them near the opening of the oviduct (Hanlon *et al*. 1994; Hanlon *et al*. 1997; Hanlon *et al*. 2002; Sauer *et al*. 1992). This is known as "male-parallel" mating (Hanlon *et al*. 1994; Hanlon 1998; Hanlon *et al*. 2002). "Male-sneak" mating, a form of head-to-head mating first observed by Hanlon *et al*. (1994), occurs when a small sneaker male jets in very quickly to an already formed pair. The sneaker grasps the female from the front and presumably places spermatophores directly onto the egg strand where it is held in her arms (Hanlon *et al*. 1994; Hanlon 1998; Hanlon *et al*. 2002) before quickly jetting off. This is known as an extra-pair copulation (Hanlon *et al*. 2002) and happens so swiftly it occurs without resistance from the paired consort male (Hanlon 1998). After mating, the female moves down to the communal egg bed (egg laying zone in Fig. 4), accompanied by the large consort male, to deposit her fertilized egg strand (Hanlon *et al*. 1994; Hanlon 1998; Hanlon *et al*. 2002; Sauer *et al*. 1992; Sauer and Smale 1993). The pair then quickly jets off back through the agonistic zone to the mating zone (Hanlon *et al*. 2002) where pairing and mating continue.

Interestingly, the majority of mature female squid caught inshore (Augustyn 1990; Hanlon *et al*. 1994; Hanlon 1998; Hanlon *et al*. 2002) and offshore (pers. comm. from Augustyn in Sauer *et al*. (1992); Sauer and Smale 1993) contain stored spermatophores within their buccal membrane. Head-to-head mating is thought to be the only way in which spermatophores can be placed within a females' buccal membrane (Hanlon *et al*. 1994). Besides the form of head-to-head mating used by sneaker males during extra-pair copulations, previously referred to as "male-sneak" mating, head-to-head mating between a large consort male and the paired female has not yet been observed inshore (Hanlon *et al*.

1994; Hanlon 1998; Hanlon *et al*. 2002). This implies head-to-head mating occurs offshore (Fig. 4) (Hanlon 1998).

Visual signalling by way of chromatophoric (Hanlon *et al*. 1994; Hanlon *et al*. 2002; Sauer *et al*. 1992), postural (Hanlon *et al*. 1994; Hanlon *et al*. 2002) and locomotor (Hanlon *et al*. 1994; Hanlon *et al*. 2002) communication is essential to the entire process of pairing and mating. Such visual signals are also important in the acquisition or guarding of a female by way of agonistic bouts between males (seen in the agonistic zone in Fig. 4) (Hanlon *et al*. 1994; Hanlon 1998; Hanlon *et al*. 2002; Sauer *et al*. 1992; Sauer and Smale 1993). Paired consort males spend a significant amount of time defending the female from rival males whereas lone males spend the majority of their time trying to become consort males (Hanlon 1998). This suggests good visibility is crucial to the formation of a spawning aggregation.

Different spawning aggregations in an area are not discrete units and there is a continual immigration and emigration of squid to and from spawning sites, and also considerable movement between the inshore spawning grounds and adjacent offshore feeding grounds (Hanlon 1998; Hanlon *et al*. 2002; Lipinski 1994; Lipinski *et al*. 1998; Sauer 1995a; Sauer *et al*. 1997; Sauer *et al*. 2000). This movement is depicted in the transitory zone in Figure 4.

Both scientists and fishers believe the environment plays an important role in the formation of *L. reynaudii* spawning aggregations inshore and hence the abundance of chokka squid and catches (Roberts 1998). The re-use of spawning sites suggests specific environmental requirements for spawning (Augustyn *et al*. 1994). For example, a common phenomenon on the south coast is intermittent coastal upwelling at prominent capes, resulting from winds with a strong easterly component (Schumann *et al*. 1982). These upwelling events bring cold, and often cleaner (Roberts 1998), water on to the inshore spawning grounds. Interestingly the increase in frequency and intensity of these upwelling events (Schumann *et al*. 1982) coincides with the peak spawning period of *L. reynaudii*, November through to February. Understanding the relationship between such environmental conditions and catches is the first step to developing catch and recruitment forecast measures and has been the focus of many studies.

Augustyn (1989) was the first to suggest sea temperature to be an important factor affecting the abundance of squid inshore and hence the availability of squid to the jig fishery, which is limited to depths <60 m. He proposed the favoured temperature range of spawning *L. reynaudii* to be between 14 and 21.5 °C and that the distribution of squid inshore was influenced by temperature and wind factors. Sauer *et al*. (1992) suggested this favoured temperature range governs the geographical limits of the inshore spawning grounds. Sauer *et al*. (1991) found a correlation between commercial squid catches and sea temperatures suggesting wind induced upwelling enhanced daily catches. However, catches were found to decrease at temperatures consistently below 11 °C and above 21 °C. It was proposed that the formation of inshore spawning aggregations was primarily dependent on environmental cues and it was important to consider other independent variables such as currents, turbidity, oxygen and swell height. Roberts and Sauer (1994) also highlighted the fact that upwelling positively influenced squid catches. They suggested that bottom turbidity was also an important variable affecting spawning aggregations due to reduced visibility. As previously mentioned, visual signalling is essential to the process of pairing and mating.

Further investigation into the effect of environmental variables on spawning aggregations was conducted by Roberts (1998). He put forward wave height, turbidity and sea temperature to be key parameters in controlling and determining spawning success. During his study, the formation of a spawning aggregation coincidently with an upwelling event led to the conclusion that upwelling may actually trigger spawning. Schön (2000), using a portable CTD deployed from a commercial fishing vessel, found a positive relationship between wind-induced upwelling and squid catches. The correlation between temperature and catch was generally negative with higher catches associated with a temperature range of 13 to 18 °C. This statistical approach showed squid catches were highest during strong easterly winds (causing upwelling), sea surface temperatures in the region of 15.0 to 16.9 °C and zero turbidity levels. He also suggested that upwelling triggered spawning whereas high turbidity levels resulted in the termination of spawning. Dorfler (2002), using a number of case studies, investigated the effect of turbidity levels on squid catches in considerable detail. Although she did find squid catches decreased with increased turbidity, she concluded it was more likely an interaction between turbidity and temperature affecting commercial squid catches. She found that when temperatures were stable between 14 and 16 °C, high turbidity negatively impacted catches whereas temperatures <10 °C and >20 °C negatively impacted catches.

From the above, it would appear that there is indeed a favoured temperature, in the region of 13 to 17 °C, for mating and spawning. Findings indicate spawning to be most intense during mild upwelling events and possibly such events, resulting in a drop of bottom temperature into the hypothesized favoured temperature range, triggering spawning activity. This was indeed the case in the study conducted by Roberts (1998) where sea surface temperature dropped from just above 16 to 13.5 °C over a period of 12 hours. As temperature started dropping, a spawning aggregation formed. On the other hand, temperature extremes of <10 °C or >20 °C, experienced during strong upwelling and downwelling events, seem to negatively impact catches (Dorfler 2002), indicating a disruption in or a termination of spawning activity.

An important characteristic of the research undertaken thus far is that it made use of indirect methods to investigate the effect of the environment on spawning and hence catches. This study, taking a more direct approach, used acoustic telemetry to monitor individual squid within spawning aggregations and their immediate response to environmental changes. This was achieved by simultaneously monitoring certain environmental variables within the study area. It was necessary to first determine the integrity of the acoustic array used in this study (Chapter 3) as well as the general oceanography of the study site (Chapter 4) to enable an accurate interpretation of results obtained (Chapter 5). The findings of this study and recommendations for future research have been summarized in Chapter 6.

CHAPTER 3

Chapter 3 of this dissertation is a collaboration between two students, Nicola Downey (MSc-Nelson Mandela Metropolitan University) and Larvika Singh (PhD-Rhodes University). As Chapter 3 investigates the integrity of an acoustic array used in the study of chokka squid *Loligo reynaudii* (Nicola Downey) and its' predators (Larvika Singh), data was collected, analysed and prepared for publication by both students. This is to certify that both students contributed equally to the calibration study. First authorship for the paper was determined by tertiary education level, hence L. Singh is first author and N. Downey second author.

Signatures

Michael Roberts	Malcolm Smale
(Supervisor)	(L. Singhs' Supervisor)
Larvika Singh	Nicola Downey
(PhD Student)	(MSc Student)

Design and calibration of an acoustic telemetry system subject to upwelling events

3.1. Introduction

As previously mentioned, this study involves the use of acoustic telemetry equipment (acoustic transmitters, stationary receivers and receivers for active tracking). Due to the dynamic environment of the inshore spawning grounds, it was necessary to test the functioning of the acoustic telemetry system under varying environmental conditions by way of range tests. Range testing defines the detection area of an acoustic receiver and is necessary information for the design of telemetry systems. The detection area is specific to the power output of the transmitters used, detection characteristics of the receiver and local factors (geophysical conditions and acoustic noise) (Pincock and Voegeli 2002) that influence acoustic transmission. Acoustic array design relies on accurate measures of detection range so receivers can be placed to provide 100 % or near 100 % detection efficiency. Apart from range testing, it is also necessary to determine the maximum number of transmitters an acoustic array can accommodate at one time.

A review of previous telemetry studies has shown diverse methods of calibrating telemetry systems and in particular receiver/transmitter range. Simpfendorfer *et al*. (2002) moored eight *Vemco* V16 RCODE acoustic transmitters at varied distances from a VR1 receiver for four days and showed a significant negative linear relationship between the daily number of detections and distance from the receiver with a maximum range of 600 m. Egli and Babcock (2004) tested range by placing *Vemco* V16 and V8 SC transmitters at fixed distances from a *Vemco* VR2 receiver for a week. Maximum range was found to be ≤500 m for both types of transmitters. Humston *et al*. (2005) towed an activated *Vemco* V16 transmitter along a route of *Vemco* VR2 receivers during low, mid and high tidal stages on Hurricane Flat, Florida. The ranges of the VR2 receivers in this system were found to be 230 and 750 m, depending on the location of the VR2 receiver. Brooking *et al*. (2006), using *Vemco* V16 transmitters and

Vemco VR2 receivers, found receiving ranges to be >500 m and so placed VR2 receivers 380 m apart to eliminate acoustic shadows ("acoustic dead zones").

Another method used to test range is to drop a tag on the sea floor and lower a receiver into the water at various stations. The results from one such *Lotek* telemetry study indicated listening stations needed to be placed 463 m apart (Windle and Rose 2005). Interestingly Robichaud and Rose (2003) used this same method and equipment, in the same location, and found the receiving range to be 960 m. This highlights the inherent variability of underwater acoustic telemetry systems, specifically the influence of environmental conditions. Hogan (2003) tested the range of five different *Lotek* transmitters and two types of receivers and found the receiving range of the radio transmitters used to be 384-813 m whilst those of the ultrasonic transmitters were 1400-2200 m.

A number of studies have simply used the ranges provided in manufacturers' specifications. For example, Welch *et al*. (2004) used *Vemco* V8SC-2L and V8SC-6L transmitters to tag Steelhead smolts. The factory specified detection range of *Vemco* VR2 receivers when using these tags is 500 m and so for this study VR2 receivers were placed 850 m or less apart. Girard *et al*. (2004) also used the manufacturer specified range while tracking acoustically tagged tuna from a vessel. They assumed when a signal was detected the tuna was within 500 m of the vessel.

Initial range tests carried out in Kromme Bay (Fig. 5) in 2003 involved simple drift tests using an inflatable boat. Transmitters were deployed on a line still attached to the boat. Starting at the same site as a moored VR2 receiver, the boat was allowed to drift until a distance of approximately 1 km from the receiver was reached. These tests showed the receiving range of the *Vemco* telemetry system to be <500 m. From this it was decided to place seven *Vemco* VR2 receivers on and around an active spawning bed 500 m apart in a hexagonal array (Fig. 13). This hexagonal configuration was used to allow for the overlap of VR2 receiving ranges and so maximise the likelihood of detecting acoustically tagged animals present within the array. The experimentation reported in this chapter had two aims: The first was to determine the range of *Vemco* VR2 receivers in various sea conditions at the study site (Kromme Bay) and hence the integrity of the hexagonal configuration. The second was to determine the effect of transmitter collisions on the number of detected signals (i.e. system saturation) and hence the ideal number of transmitters to use simultaneously.

3.2. Materials and methods

Four calibration experiments were undertaken in Kromme Bay in 2006 and 2007, two using V9 and V16 transmitters with random off times under isothermic (21 June 2006) and thermocline conditions (23 November 2006) and two using a fixed off time V9 pinger under isothermic conditions (3 and 18 November 2007).

3.2.1. Site Description

Kromme Bay is a semi enclosed log spiralled embayment on the western side of St Francis Bay (Fig. 5). It is relatively sheltered from the winter south-westerly swells and winds, and has a gentle sloping sea floor (Birch 1981). The bottom consists mainly of rippled coarse sand interspersed with rock and low relief reef (Roberts 1998). The bay is commonly used as spawning grounds by the chokka squid *Loligo reynaudii* and was the chosen study site for the acoustic telemetry experiment reported on in Chapter 5.

3.2.2. Acoustic Telemetry Equipment

All acoustic telemetry equipment was purchased from *Vemco* (Ltd. Nova Scotia, Canada). Two VR2 omnidirectional receivers (Series 2) and a VR100 (a receiver used for manual tracking) with an omnidirectional hydrophone were used to detect transmitters. Five types of transmitters were used during the range and system saturation tests, those used to tag squid and those used to tag predators. The reason being, predator acoustic telemetry experiments were conducted simultaneously and in the same area as the current study being reported on in this dissertation. The transmitters used are shown in Table III.

Table III: Transmitter types and specifications.

Transmitter type	Number used	Min-max off times (s)	Pressure sensor	Used to tag
V9P-6L-S256	8	30 - 90	Yes	Squid
V9 Pinger	1	Fixed at 10	No	NA
V9-6L-RO4K	2	20 - 69	No	Predators
V9P-2H-S256	2	20 - 60	Yes	Predators
V16-5H-RO4K	2	35 - 109	No	Predators

3.2.3. Environmental Monitoring

All meteorological data for the current study was obtained from the South African Weather services (2006, 2007)[IV]. Water temperature data for 2006 was obtained from three different sources: On the 23 November 2006, a full temperature profile was recorded using a portable CTD (Seabird 19 Plus). This equipment was not available on the 21 June 2006 and temperature data was extracted from a permanent thermistor array moored 50 m from the squid buoy in Kromme Bay (Fig. 5 and Fig. 6). Star-oddi Starmon mini underwater temperature recorders (UTR's) at depths of 9, 14, 21 and 24 m were used to obtain a temperature profile, with information on surface temperature obtained via archival remote satellite sensing (Marine and Coastal Management 2006[V]). Temperature data for the 2007 range tests were obtained from a minilogger lowered through the water column at 1 m.sec^{-1}. Visibility from the surface was measured with a secci disc.

3.2.4. Range Testing

A VR2 receiver was moored 2 m off the bottom (bottom depth 17.1 m) at Position 1 (Table IV) on the calibration line shown in Fig. 6. A single V9P-6L-S256 tag (referred to hence forth as a "squid tag", Table III) was placed within the weave of a hollow core polypropylene ski rope that was anchored to the seabed. A subsurface float was attached to keep the rope vertical in the water column. The transmitter was deployed at Position 1 i.e. 0 m from the moored VR2 receiver, 2 m from the bottom, for 10 minutes. The rope and transmitter were retrieved and the entire process repeated at Positions 2 to 8 (Table IV). A sea anchor was deployed from the boat to keep the boat as close to the deployed transmitter as possible without the use of the motors. The boats echosounder was also switched off to eliminate possible interference with the receiver. On the 23 November 2006, a VR100 was lowered over the side of the boat to record the number of signals transmitted per 10 min period. This experiment was conducted in isothermic (21 June 2006) and thermocline (23 November 2006) conditions.

[IV] South African Weather Service. 2006, 2007. Weather data.

[V] Marine and Coastal Management 2006. Satellite Sea Surface Temperature Data.

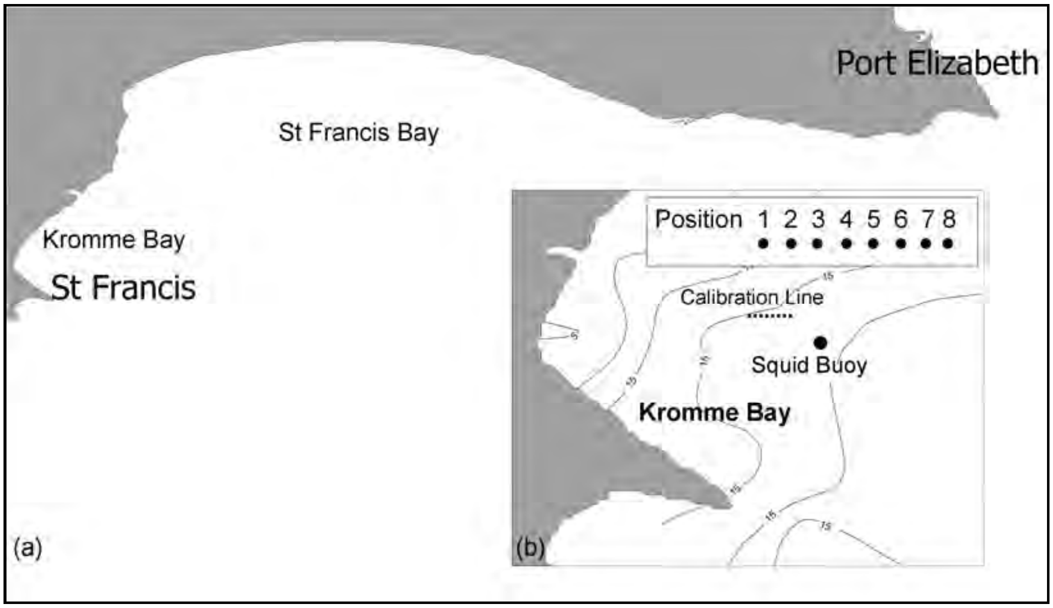


Figure 5: A map depicting (a) St Francis Bay, South Africa and (b) the position of the calibration line in Kromme Bay. Also illustrated is the position of the squid buoy in Kromme Bay. Contour lines depict the bathymetry of Kromme Bay.

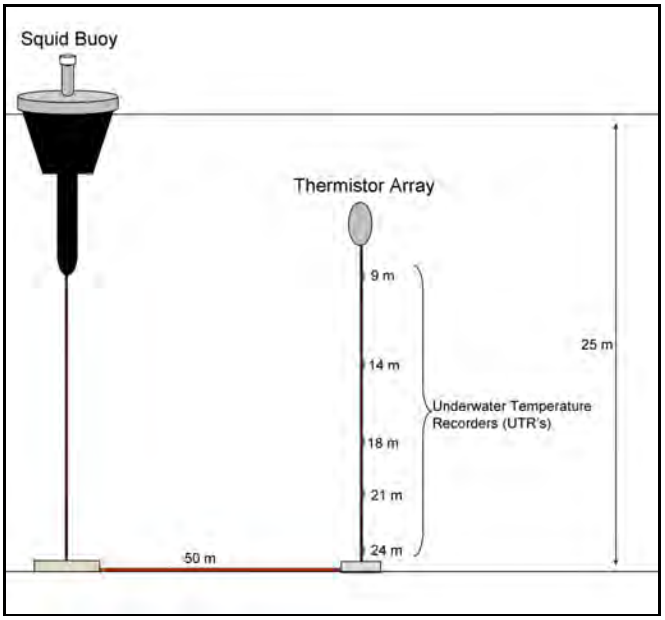


Figure 6: The design of the thermistor array moored 50 m from the squid buoy in Kromme bay as part of a current long-term monitoring project.

Table IV: Distances of the positions used from the VR2 receiver moored in Kromme Bay.

Position	Distance from moored VR2 (m)
1	0
2	75
3	150
4	225
5	300
6	375
7	450
8	500

The average time interval between signal transmissions was determined using the min-max off times of the V9P-6L-S256 coded sensor transmitters. The average length of a signal transmission was calculated from the VR100 files generated on the 23 November 2006 and added to the average time interval between transmissions. This enabled the mean number of detections in a ten minute period to be calculated, truncated and compared to the actual number of signals detected by the moored VR2 receiver.

The experiment was later repeated on the 3 and 18 November 2007 under isothermic conditions using a V9 continuous pinger with a fixed off time of 10 sec. The transmitter with the fixed off time was tested at 0 m from the VR2 receiver and thereafter at 50 m increments until 500 m from the receiver.

3.2.5. System Saturation

The range test as described in the previous section was repeated on the 21 June 2006 and the 23 November 2006 with four "squid tags", eight "squid tags" and 14 transmitters (eight "squid tags" and 6 "predator tags", Table III) deployed simultaneously. All transmitters were placed within the hollow core of the rope at 0.5 m intervals (Fig. 7). A second VR2 receiver (2 m below surface) and a VR100 hydrophone (1.5 m below surface) where lowered over the side of the boat. The total number of signal detections was taken as the sum of detections recorded by one or more of the receivers (moored VR2 receiver, VR100 or VR2 receiver attached to boat). The total number of detections recorded at 0 m was plotted for one, four and eight and 14 transmitters. Also plotted was the number of detections recorded by the moored VR2 receiver at Positions 1 through to 8 (Table IV) for eight “squid” tags and for 14 tags (separating squid and predator tags) in thermocline and non-thermocline conditions.

3.3. Results

3.3.1. Environmental conditions

On the 21 June 2006, the water column was well mixed with surface and bottom temperature differing by only 0.66 °C (Fig. 7). On the 23 November 2006, a thermocline was recorded at six meters with temperatures decreasing from 18.4 °C to 13.4 °C (Fig. 7). On both occasions, wave height increased through the day to a maximum of 1.5 m. Water visibility on both days was approximately 5 m. On the 21 June 2006, a strong south-westerly wind of ~20 kts persisted throughout the day, and 17 mm of rainfall was recorded. On the 23 November 2006, a light north-easterly breeze became a south-easterly to easterly wind of 5 kts, with no rainfall. On both days wind speeds gradually increased from morning to late afternoon.

Environmental conditions during the 2007 range tests were similar on both days. The water column was well mixed and no thermocline was present on either day. The wind speed for both days varied between 4 and 6 $m.s^{-1}$. Visibility on the 3 November 2007 was 5 m with a south-westerly wind blowing and on the 18 November 2007, a north-easterly wind was present with 8 m visibility.

3.3.2. Range testing

Range testing was carried out in both an isothermal (21 June 2006, 3 November 2007 and 18 November 2007) and a stratified (23 November 2006) water column (Fig. 7) Data plotted in Figure 8 illustrates how range and a thermocline affected the number of signals detected by the VR2 receiver as tag distances increased from 0 to 500 m from the VR2 receiver. Theoretically, an average of nine signals should have been recorded from the V9P-6L-S256 transmitter over this distance until the range limit was reached (Fig. 8a). The VR100 recorded varied numbers of detections in comparison to the moored VR2 receiver on both the 21 June 2006 and the 23 November 2006. Initially at 0 to 150 m, the VR100 recorded fewer detections than the VR2 receiver even though the VR100 was always placed next to the transmitters. Interestingly, from 225 to 500 m the VR100 showed a decrease in the number of detections (Fig. 8a).

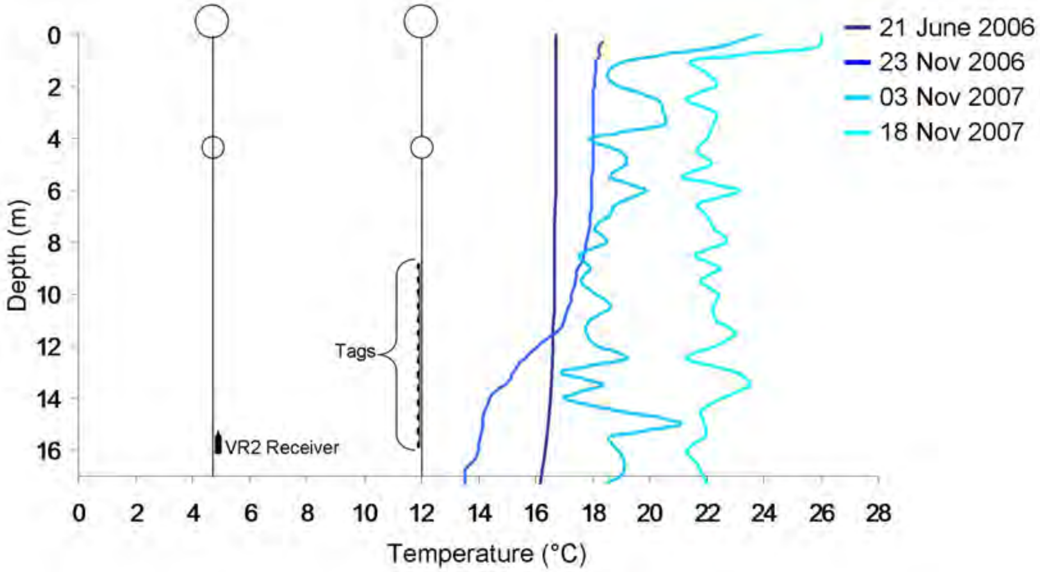


Figure 7: Temperature profiles for the 21 June 2006, 23 November 2006, 3 November 2007 and the 18 November 2007. Also illustrated is the mooring design used for the moored VR2 receiver and the position of the transmitters inserted into the hollow core of the rope at 0.5 m intervals, drawn to scale.

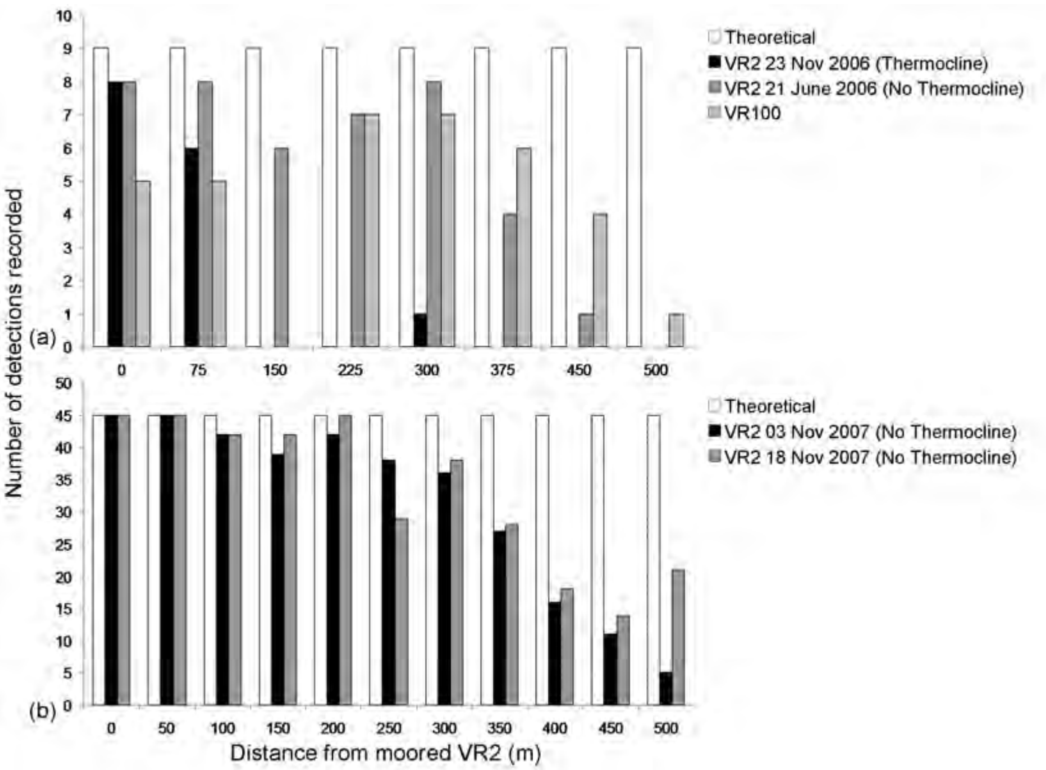


Figure 8: The number of detections recorded by the moored VR2 receiver as distances between the VR2 receiver and the (a) V9P-6L-S256 transmitters and the (b) V9 pinger increased from 0 to 500 m in (a) thermocline and (a and b) isothermic conditions. Also plotted is the theoretical number of signals expected and the number of signals recorded by the VR100 suspended over the side of the boat on the 23 November 2006 (a).

On the 21 June 2006 when no temperature gradient existed, eight detections were recorded at 0, 75 and 300 m from the moored VR2 receiver (Fig. 8a). Six and seven detections were recorded at 150 and 225 m respectively. At distances greater than 300 m the number of detections showed a sharp decrease. These results were unexpected as a similar number of detections should be recorded until the range limit is exceeded. At 375 and 450 m, only four and two detections were recorded respectively. No detections were recorded at 500 m indicating a range limit of 450 m. This was despite potential noise from rainfall on the sea surface. For the purpose of the squid-predator telemetry study receiver range can therefore be taken as 300 m in isothermal conditions as at this distance more than 50 % of the potential number of signals is detected. Beyond this point the decrease in the number of signal detections is too great. The results from the V9 pinger with a fixed off time, also tested in isothermic conditions, indicate a range of 350 m (more than 50 % of potential signals detected) (Fig. 8b). This result is similar to the range test using the V9P-6L-S256 transmitter with a random off time.

The range test showed very different results on the 23 November 2006 in the presence of a thermocline (Fig. 8a). At 0 m, the same number of detections was recorded as on the 21 June 2006. At 75 m however, the number of signals recorded dropped to six with no detections recorded at 150 and 225 m. Surprisingly one detection was recorded at 300 m. No detections recorded beyond this distance suggests a range limit (point where more than 50 % of the potential number of signals detected) of 75 m in thermocline conditions.

For both sets of conditions a clear decrease in detections with increasing distance was evident. The water column stratification exacerbates this effect. It is interesting that in both cases relatively fewer signals were recorded at 150 and 225 m.

Results from the fixed off time V9 Pinger were similar to those of the random off time V9P-6L-S256 transmitter during isothermic conditions (Fig. 8b). The maximum number of detections was recorded at 0 and 50 m (Fig. 8b). From 75 m there was a gradual decrease in signal detections until 300 m from the VR2 receiver (Fig. 8b). After 350 m there was a sharp decrease in signal detections with fewer than 50 % of transmitted signals being detected (Fig. 8b).

3.3.3. System Saturation

Figure 9 illustrates the actual number of signals recorded by a VR2 receiver when an increasing number of transmitters was deployed 0 m from the VR2 receiver. A significant decrease in the number of signal detections was observed when increasing the number of transmitters from eight to 14. With eight transmitters in the water the total number of signal detections was 41. The inclusion of the "predator tags" (14 transmitters in total) resulted in the recording of only 38 signals at 0 m. Despite using a greater number of tags, the increase in frequency of signal collisions resulted in fewer signals being detected and recorded.

Figure 10 shows the overall performance of a system comprising of a single VR2 receiver and eight "squid tags". As noted in other studies Simpfendorfer *et al*. (2002) the number of signal detections decreased almost linearly with distance to a detection limit of ~450 m in isothermal conditions. The presence of a thermocline however, caused the number of signal detections to decrease with an exponential trend resulting in a technical detection limit of ~300 m.

The effect of the "predator tags" on saturation of the system in thermocline and non-thermocline conditions is given in Figure 11. The "squid" and "predator tag" detections in a stratified water column (Fig. 11a) were equal up to 300 m from the moored VR2 receiver. Between 375 and 450 m, the "predator tags" were recorded more often than the "squid tags". In the presence of a thermocline (Fig. 11b), "squid" and "predator tag" detections were equal up to 75 m from the VR2 receiver. At a distance of 150 m only one of 13 detections came from a "squid tag". Beyond 225 m, "predator tags" were the only transmitters detected.

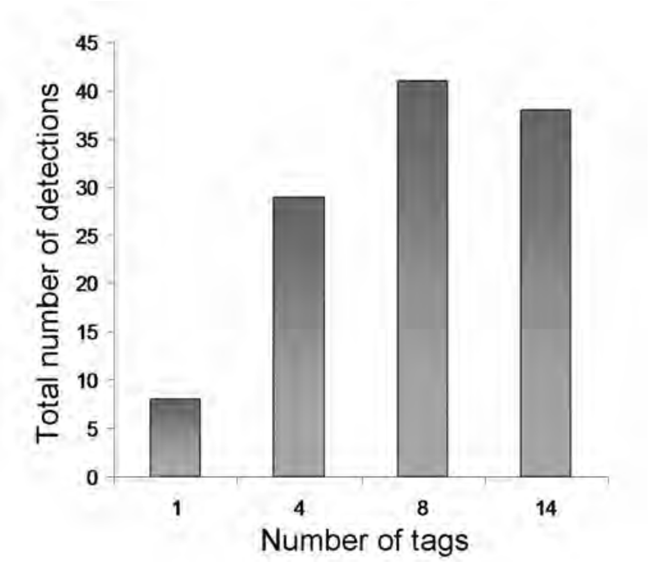


Figure 9: The number of detections recorded by the moored VR2 receiver when an increasing number of transmitters were deployed at Position 1 (0 m) from the VR2 receiver.

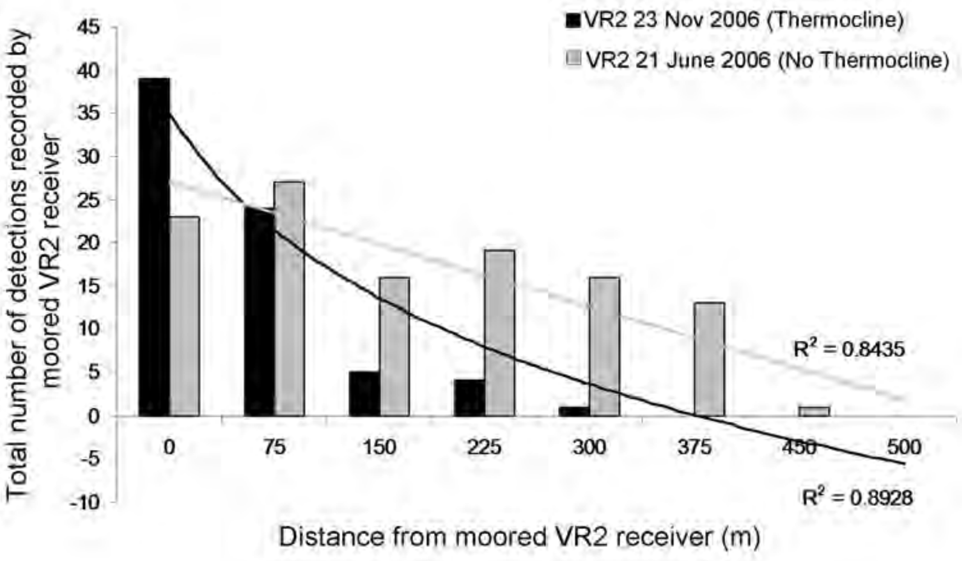


Figure 10: The number of detections recorded by the moored VR2 receiver as eight V9P-6L-S256 transmitters were moved increasing distances from the VR2 receiver.

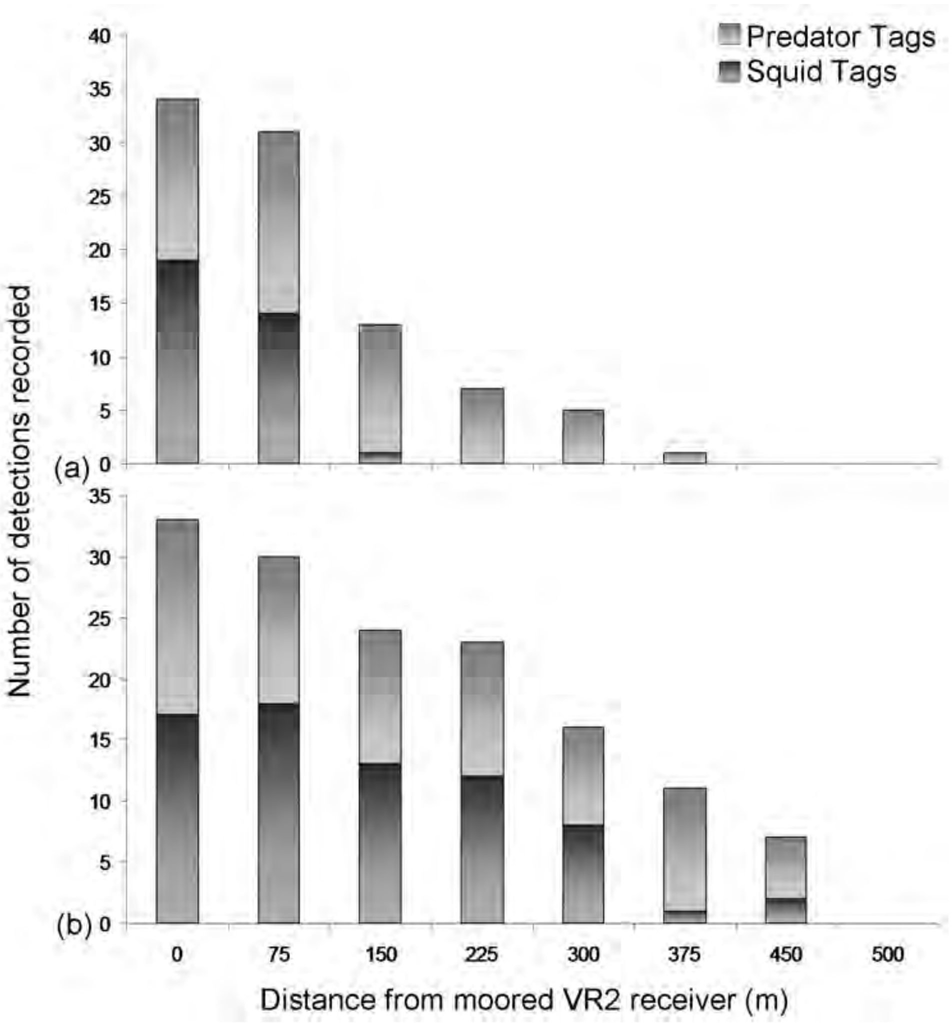


Figure 11: The effect of the "predator tags" on system saturation in (a) isothermic and (b) thermocline conditions.

3.4. Discussion

3.4.1. Range Testing

The first aim of this work was to determine the detection range of a VR2 receiver using a single V9 transmitter. It should be pointed out that signals transmitted become weaker over distance as energy is lost by way of spherical spreading, absorption, refraction and reflection (Pincock and Voegeli 2002). Thermoclines are physical features that introduce some of these effects (Heupel *et al*. 2006). In theory, if a signal is propagated from a transmitter below the thermocline, the signal strength should be contained in that bottom layer and little energy lost if the receiver is also placed below the thermocline. Signals transmitted above the thermocline should therefore be weakest owing to reflection. This is however not the case as demonstrated in Figure 12. Signal transmissions from these transmitters are omnidirectional and signal strength is reduced as a result of not only thermoclines but reflection, refraction, absorption and interactions with other propagated signals and the substrate.

Thermoclines on the Agulhas Bank are caused by cold bottom water being pulled up to the shelf into shallower coastal regions (Roberts and van den Berg 2002). In Kromme Bay, upwelling events are a regular occurrence during the summer months, November through to February (Dorfler 2002), and are forcedly increased in both frequency and intensity by north-easterly winds (Roberts and Sauer 1994; Sauer *et al*. 1991). Thermoclines are less prevalent in winter months as the region is dominated by strong westerly winds which cause mixing of the water column (Schumann *et al*. 2005). Since the squid-predator acoustic telemetry study is conducted during the months of October and November, the effect of thermoclines on the functioning of the acoustic telemetry system is an important factor that needs to be considered.

The behaviour of the animal or animals tagged is an essential consideration when designing an acoustic telemetry array (Heupel *et al*. 2006). In the case of *Loligo reynaudii*, spawning occurs in typically shallow water of 20-30 m. Large aggregations made up of thousands of male and female squid are formed. Boat echo sounders show the aggregation to have a "mushroom" shape (Sauer *et al.* 1997). A previous study of the spawning behaviour of *L. reynaudii* showed pairing and mating to occur in the bottom 10 m after which the female squid, accompanied by the male, moved to the substrate to deposit her eggs (Sauer *et al.* 1997). The chosen placement of the moored VR2 receiver 2 m off the bottom and the transmitters near to the substrate (Fig. 7) during the current study was a design feature to take into account the near benthic and benthic activity.

The overall trend of a decrease in signal detections as the transmitter was moved further away from the moored VR2 receiver (Fig. 8) is similar to that of other telemetry studies and although the declining relationship should theoretically not occur, it has been reported regularly (Heupel *et al.* 2005). The further the signal has to travel, the more likely is loss of signal energy and hence fewer signals are successfully detected. A possible reason for this trend is sound travels at shorter distances when the sea substrate is comprised of soft sediment. This type of substrate may absorb the signal from transmitters (Heupel *et al.* 2006). It is necessary to determine whether or not a specific study site follows this declining detection trend and set the acoustic array accordingly. Signal detections were only significantly lower over distance when the water column was stratified (Fig. 8a). The VR100 used to record this variation however, in some cases detected fewer signals than the moored VR2 receiver (Fig. 8a). This was attributed to the hydrophone of the VR100 being suspended 1.5 m below the water surface and hence above the thermocline whereas the VR2 receiver was below the thermocline.

An unexpected anomaly in the data was the loss of signals at 150 m and 225 m during both the 21 June 2006 and 23 November 2006 range tests. As this loss of signals occurred during both thermocline and isothermic conditions, a possible cause could be substrate type at these positions (Positions 3 and 4, Table II). For example, patches of reef could have influenced the propagation of signals (Heupel *et al.* 2006). It is common to find egg beds interspersed between patches of reef in Kromme Bay. Future experiments should map the seabed below the study site in order to determine the effect of bottom topography on receiver range.

Wind is also known to influence the propagation of signals in underwater acoustic telemetry systems. Recently, a *Vemco* 69 kHz Sea Water Range Calculator software tool was released on the *Vemco* website[VI]. This software calculates the range of transmitters based on transmitter power in typical ocean conditions (Table V). The simulated increase in wind speed indicates the loss of signal detections which was not seen in the range testing conducted here (Fig. 8). Wind it seems has a minimal effect on signal detection for this particular acoustic array due to the depth at which the equipment is placed, but highlights that all aspects of the system need to be considered.

Table V: The ranges of the tags used in this study as generated by the *Vemco* 69 kHz Sea Water Range Calculator tool available on the *Vemco* Website.

Transmitter type	Transmitter level	Wind speed (knots)	Range (meters)
V9P-6L and V9-6L	139 dB re 1 uPa @ 1 metre	Calm	352
		3 to 6	339
		11 to 16	247
		28 to 34	157
V9P-2H	147 dB re 1 uPa @ 1 metre	Calm	539
		3 to 6	522
		11 to 16	406
		28 to 34	282
V16-5H	159 dB re 1 uPa @ 1 metre	Calm	876
		3 to 6	857
		11 to 16	714
		28 to 34	551

In the Kromme Bay area, range seems to be heavily dependant on thermal stratification of the water column as signal detections are reduced from 300 m under isothermic conditions to 75 m when the water column is stratified. As the squid-predator acoustic telemetry study is conducted during summer when thermoclines are prevalent, detection range should theoretically be based on the worst-case scenario of 75 m.

[VI] Vemco-A division of AMIRIX Systems Inc. 2004. http://www.vemco.com

The estimation of the theoretical number of detections for the initial range tests in 2006 caused difficulties due to the pseudorandom off times. At the time of the initial calibration study however, transmitters with fixed off times were not available. Two additional range tests (Fig. 8b) were therefore conducted in 2007 using a V9 pinger with a fixed off time. The V9 pinger had the same power output as the V9P-6L-S256 transmitter used in the initial experiment. The potential number of detections in a ten-minute period could accurately determined as the length of each signal detection and the time interval between consecutive transmissions remained the same.

It is important to note that Kromme Bay is not only subject to intrusions of cold upwelled water but also frequent benthic turbidity events (Dorfler 2002). According to Pincock and Voegeli (2002) high turbidity levels will further decrease receiving ranges of the VR2 receivers as signal energy will be absorbed by suspended organic particles. In view of the dynamic environmental conditions in Kromme Bay it would be prudent to place sentinel or reference transmitters near or within the VR2 receiver array during future acoustic telemetry experiments. This would allow changes in receiver range during the study period to be monitored. System saturation needs to be considered when selecting the number and type of reference transmitters, as will be discussed below.

3.4.2. System Saturation

The inclusion of multiple transmitters into an acoustic telemetry system decreases the probability of signals being detected due to signal collisions. When coded *Vemco* transmitters transmit signals, a series of pings, known as a pulse train, is emitted. These are recorded by the VR2 receiver. When all the pings are recognised in sequence by the VR2 receiver, the pulse train is recorded as a signal detection. The overlapping of pulse trains (signal collisions) from two or more transmitters results in no signals being recorded. The frequency of overlapping of individual pings increases as more transmitters are placed within a system and fewer signals are successfully detected and recorded (Pincock and Voegeli 2002).

To reduce the occurrence of signal collisions, the *Vemco* transmitters have been programmed with a pseudorandom time delay between transmissions (i.e. the time delay between transmissions is not the same from one transmission to the next). This ensures the overlapping of signals from two transmitters will not occur again on the next transmission. Pseudorandom transmission enables the system to deal with an increased number of transmitters. Increasing the min-max off times between signal transmissions further reduces the frequency of collisions.

It is necessary to determine the maximum number of transmitters and the ideal min-max off times to use within a telemetry system to minimize the loss of transmitter data. If the off time is too long, animals could move in and out of a system undetected. It is therefore ideal to use longer off times with animals that are slow moving or resident to the study site and shorter off times for animals that move in and out of study site fairly quickly. In the VR2 receiver array discussed here, saturation occurred when eight "squid tags" were placed within the system (Fig. 9).

The reduction in detections when "predator tags" were added to the system was a result of both an increased frequency in the overlapping of pulse trains and the greater signal strength of the "predator tags". "Predator tags" were more powerful, as a result of stronger battery power, and four of these transmitters had shorter on-off times which meant the tags emitted signals more often and were more likely to clash with "squid tags".

Smaller and therefore less powerful transmitters are used on squid as they are much smaller in size than the predators and the transmitters are placed internally. For the predators, the larger V16 tags are attached externally while the smaller V9 or V13 tags are internally attached. It is important to note that any attachment to animals should not weigh more than 2 % of the animals' total weight to avoid hindering natural behaviour (Pincock and Voegeli 2002).

Although preliminary results of the squid-predator telemetry study in Kromme Bay revealed predators do not remain on the spawning beds for long periods of time, the number of tagged predators within the array should be considered to avoid the system becoming saturated.

Vemco has also released the *Vemco* Collision Calculator, another software tool on the *Vemco* website[VII]. This calculator is used as a guide to determine system saturation by calculating the total number of detections per hour and the time taken for all transmitters to be detected. Although based on standard R64K tags, the collision calculator still provides an estimate of the time taken to detect a certain number of "squid tags" within our system. Table VI gives the results generated by the *Vemco* Collision Calculator for eight, nine and ten "squid tags" with an average time delay of 60 seconds. By placing nine "squid tags" within the system at one time it is possible to record the maximum number of detections in one hour. According to the *Vemco* Collision Calculator, placing more than nine tags within the system will reduce the total number of detections per hour as collision effects become significant.

Table VI: Results generated by the *Vemco* Collision Calculator for transmitters with an average time delay of 60 seconds.

Number of tags	8
Time to detect all tags	9 min
Average update rate for each tag	2.1 min
Total detections per hour	222
Number of tags	9
Time to detect all tags	10 min
Average update rate for each tag	2.4 min
Total detections per hour	224
Number of tags	10
Time to detect all tags	12 min
Average update rate for each tag	2.6 min
Total detections per hour	223

The field results showed collision effects become significant when using eight "squid tags" as the tags are S256 coded transmitters. The Kromme Bay acoustic system is also more

---

[VII] Vemco-A division of AMIRIX Systems Inc. 2004. http://www.vemco.com complicated as more than one type of transmitter is used at a given time. However the squid and predators tend to move in and out of the array over time. By actively monitoring the number of tagged individuals within the array, using a VR100, the system can be “topped up” with newly tagged animals whenever individuals move out of the system.

3.5. Conclusions

From the above, the hexagonal configuration of VR2 receivers is deemed to be best suited to monitor the movement patterns of chokka squid and predators. However, when using the current distance between VR2 receivers (500 m), it is evident that in thermocline conditions not all tagged animals will be detected as "acoustic dead zones" as wide as 350 m may exist between receivers (Fig. 13). This is the worst-case scenario. However, if the VR2 receivers are placed closer together, only a very small area of the spawning site will be monitored. If receiving range is equal to or greater than 250 m (isothermic conditions), "acoustic dead zones" are absent. During isothermic conditions, there will be an approximate 50 m overlap of receiver range (Fig. 13). The placement of VR2 receivers is therefore a trade-off between monitoring as much of the spawning site as possible and reducing the extent of "acoustic dead zones" resulting from various environmental conditions. The results show a system such as this can support approximately seven tagged squid and two tagged predators at one time, however by using tags with longer off times; more animals can be accommodated within the system.

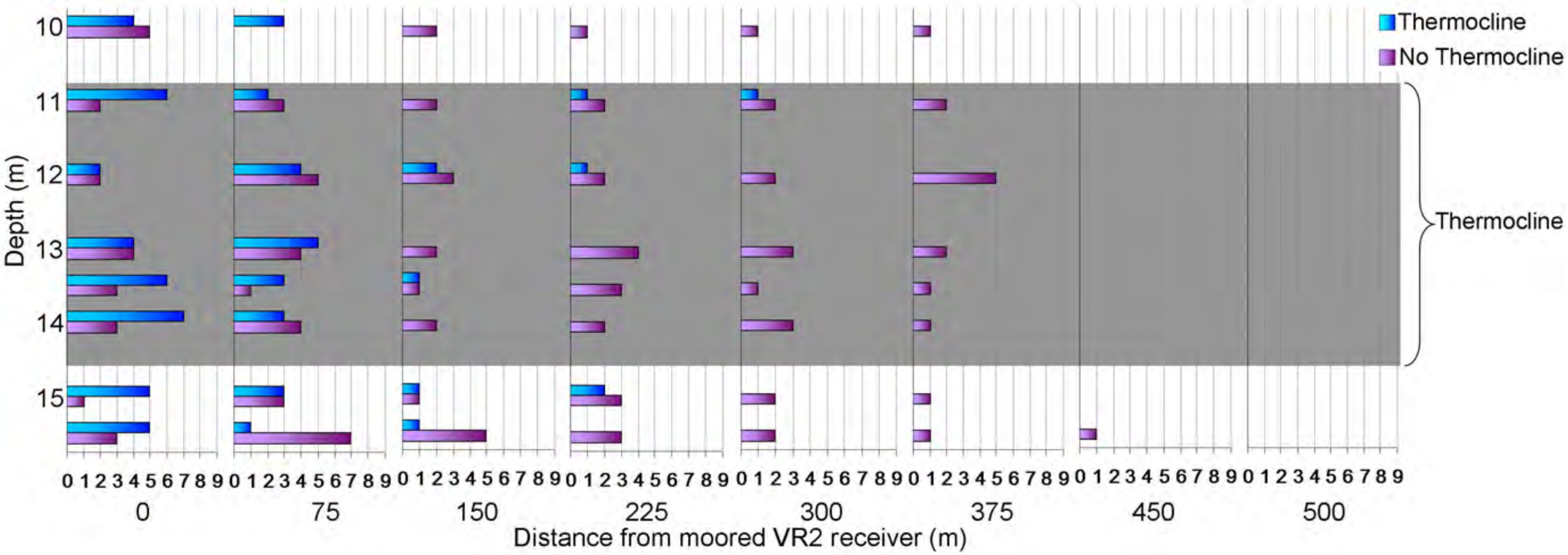


Figure 12: The number of detections recorded by the moored VR2 receiver when eight V9P-6L-S256 transmitters were deployed increasing distances from the VR2 receiver. The position of the thermocline, between 11 and 14 m, is indicated by the shaded area.

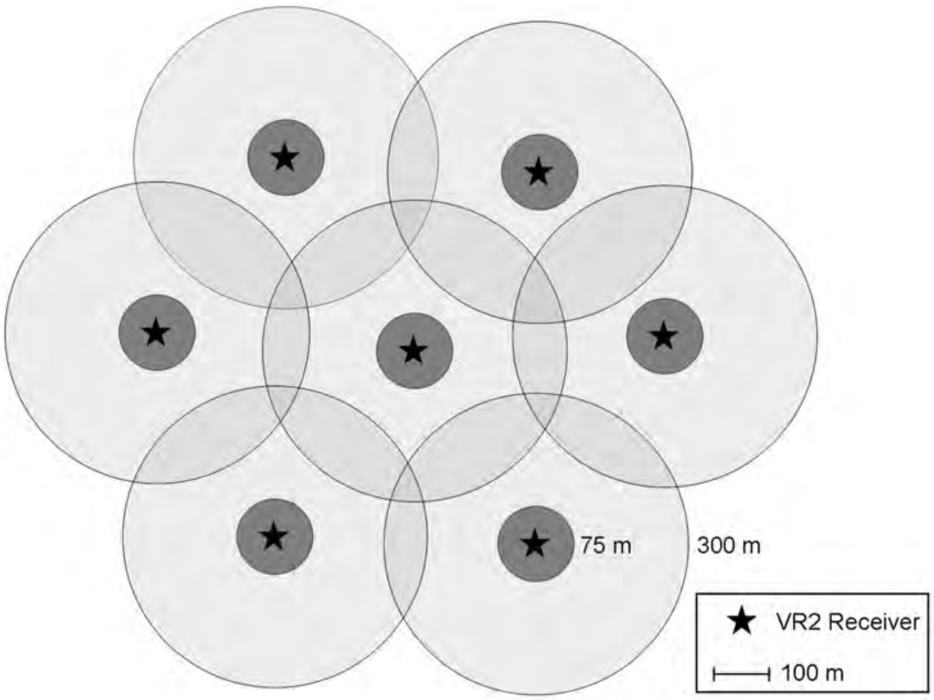


Figure 13: The hexagonal array detection range (drawn to scale) for isothermic (large circles) and thermocline (small circles) conditions.

CHAPTER 4

Oceanographic conditions in Kromme Bay

4.1. Introduction

Studies have shown Kromme Bay to have a complex circulatory system with an anticyclonic flow pattern isolated from the main flow just outside of the bay (Dorfler 2002; Roberts and van den Berg 2002). Water masses move up and down the seabed slope due to wind-induced upwelling and downwelling and the semi-enclosed circulation pattern may result in the entrapment of such water masses within Kromme Bay (Dorfler 2002). Apart from major upwelling and downwelling events, Kromme Bay is also subject to turbidity events. These events are caused by the movement of turbid water masses into Kromme Bay along with upwelled water or increased swell (Dorfler 2002). Overall, the oceanographic conditions within Kromme Bay are complex and highly variable. However, the degree of spatial variability of oceanographic events within the bay itself is not known.

The experimentation reported on in this chapter had one major aim: to investigate the spatial variation in temperature and turbidity conditions within Kromme Bay and hence determine whether environmental data recorded at the thermistor array site was an accurate indication of conditions throughout Kromme Bay.

4.2. Materials and Methods

Small boat CTD (Seabird 19 plus) surveys were conducted in Kromme Bay on five days of varying sea conditions. The date and number of stations sampled is given in Table VII. Gridded surface and bottom temperature and turbidity plots were generated from the CTD cast data using Ocean Data View (ODV)[VIII]. These ODV plots provided "snap shots" of the spatial variation in temperature and turbidity conditions within Kromme Bay.

To further investigate the spatial variation of temperature within the bay, an additional Star-oddi Starmon mini UTR was deployed in Kromme Bay (Site 1-Fig. 14) in July 2008. Hourly bottom temperature measured at this site was compared to hourly bottom temperature data recorded at the thermistor array (Site 2-Fig. 14) over a period of three months. Port Elizabeth hourly wind data for the relevant periods of the small boat CTD survey and three month temperature comparison was obtained from the South African Weather Services.[IX] A UNH Lanczos filter (weighted 73) was applied to the data and stick vector plots generated using ADCP Data Analysis Software (ADAS)[X]. Wind direction is orientated away from the axis and not towards it.

Table VII: Date and number of stations sampled during the small boat CTD survey in Kromme Bay

Date of survey	Number of stations sampled
30-Oct-2006	10
31-Oct-2006	13
10-Nov-2006	14
24-July-2008	13
27-July-2008	14

[VIII] Schlitzer, R. 2007. Ocean Data View: 3.3.2-2007. http://odv.awi.de.

[IX] South African Weather Service. 2006, 2008. Wind Data.

[X] Duncan, L.; Duncan, F. and Nelson, G. ADCP Data Analysis Software. 1.3.1.43.

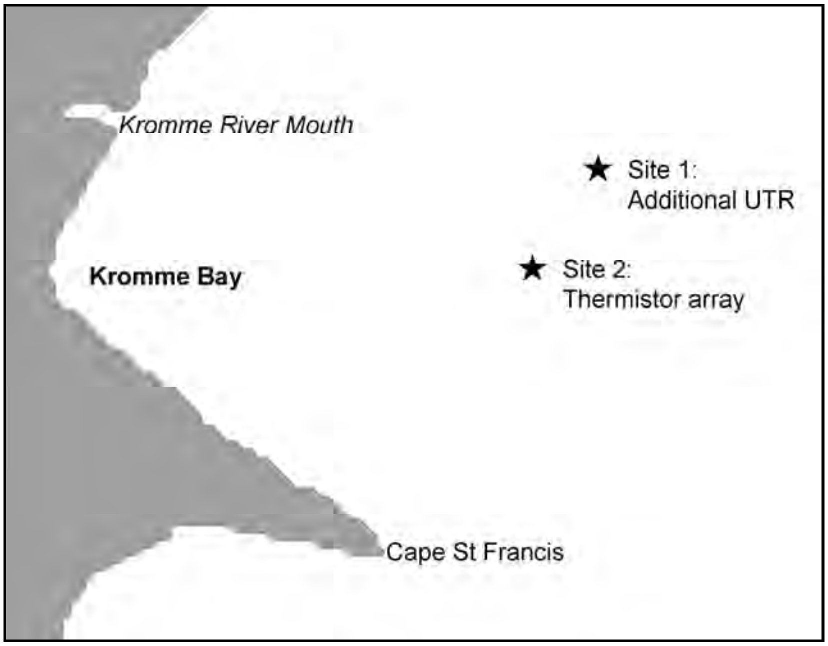


Figure 14: The position of the thermistor array (Site 2) and the additional UTR (Site 1) deployed in Kromme Bay in July 2008.

4.3. Results

A major upwelling event was recorded at the thermistor array (Site 2-Fig. 14) in Kromme Bay just prior to the small boat CTD survey conducted on the 30 October 2008 (Fig. 15a). A strong southwesterly resulted in downwelling and the warming of bottom waters. As the wind decreased in strength bottom temperature dropped again by ~2 °C. The small boat CTD surveys conducted on the 30 and 31 October 2006, were carried out while bottom temperatures slowly warmed again. The gridded ODV plots (Fig. 16b and d) show the cold upwelled water moving out of Kromme Bay as it was replaced by warmer water due to the process of downwelling. Another result of the southwesterly winds was an increase in bottom turbidity, specifically on the western side of Kromme Bay (Fig. 17b and d). On both the 30 and 31 October 2006, throughout the bay, surface temperature remained in the region of 17 °C (Fig. 16a and c) and surface turbidity levels were low (<3 NTU's) (Fig. 17a and c).

As a result of relatively weak easterly winds, bottom temperature recorded at the thermistor array site remained stable prior to and during the small boat CTD survey carried out on the 10 November 2006 (Fig. 15). Surface temperatures throughout the bay were in the region of 20 °C (Fig. 16e) whereas bottom temperatures were determined by the bathymetry of Kromme Bay, decreasing with depth (Fig. 16f).

During the small boat CTD surveys conducted on the 24 and 27 July 2008, bottom temperature recorded at the thermistor array site remained <16 °C due to weak easterly and south westerly winds (Fig. 18). Surface temperatures throughout the bay on both the 24 and 27 July 2008 remained at ~16 °C (Fig. 19a and c), as did bottom temperatures in the shallower regions of the bay, indicating the absence of a thermocline in these areas (Fig. 19b and d). Bottom temperature at ≥30 m were ~2 °C cooler (Fig. 19b and d). On the 27 July 2008, wind strength began increasing and it appears the strong westerly resulted in the movement of warmer water into the eastern part of Kromme Bay. Both surface and bottom temperatures in this area increased (Fig. 19d).

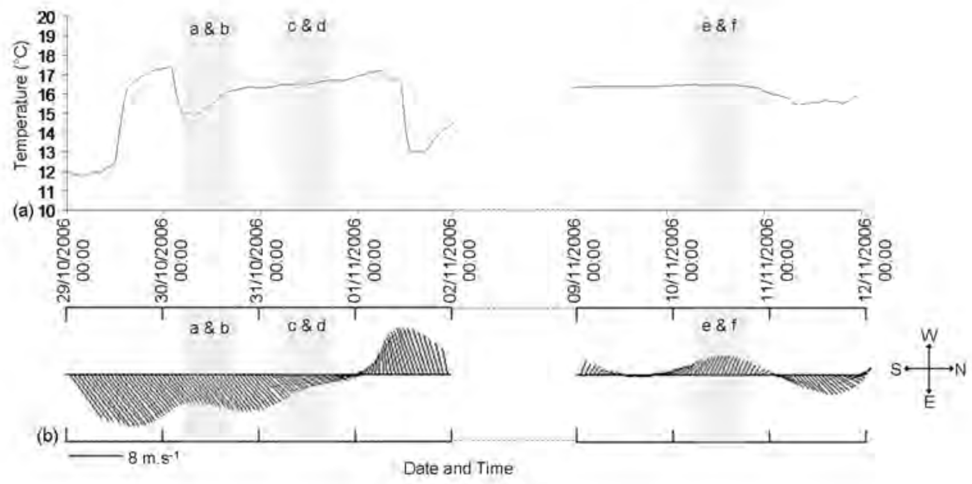


Figure 15: (a) Hourly bottom temperature recorded at the squid buoy during the small boat CTD survey in 2006 and (b) hourly wind data recorded at Port Elizabeth during the same time period. The shaded areas refer to the gridded ODV plots (a to f) in Fig. 16 and Fig. 17.

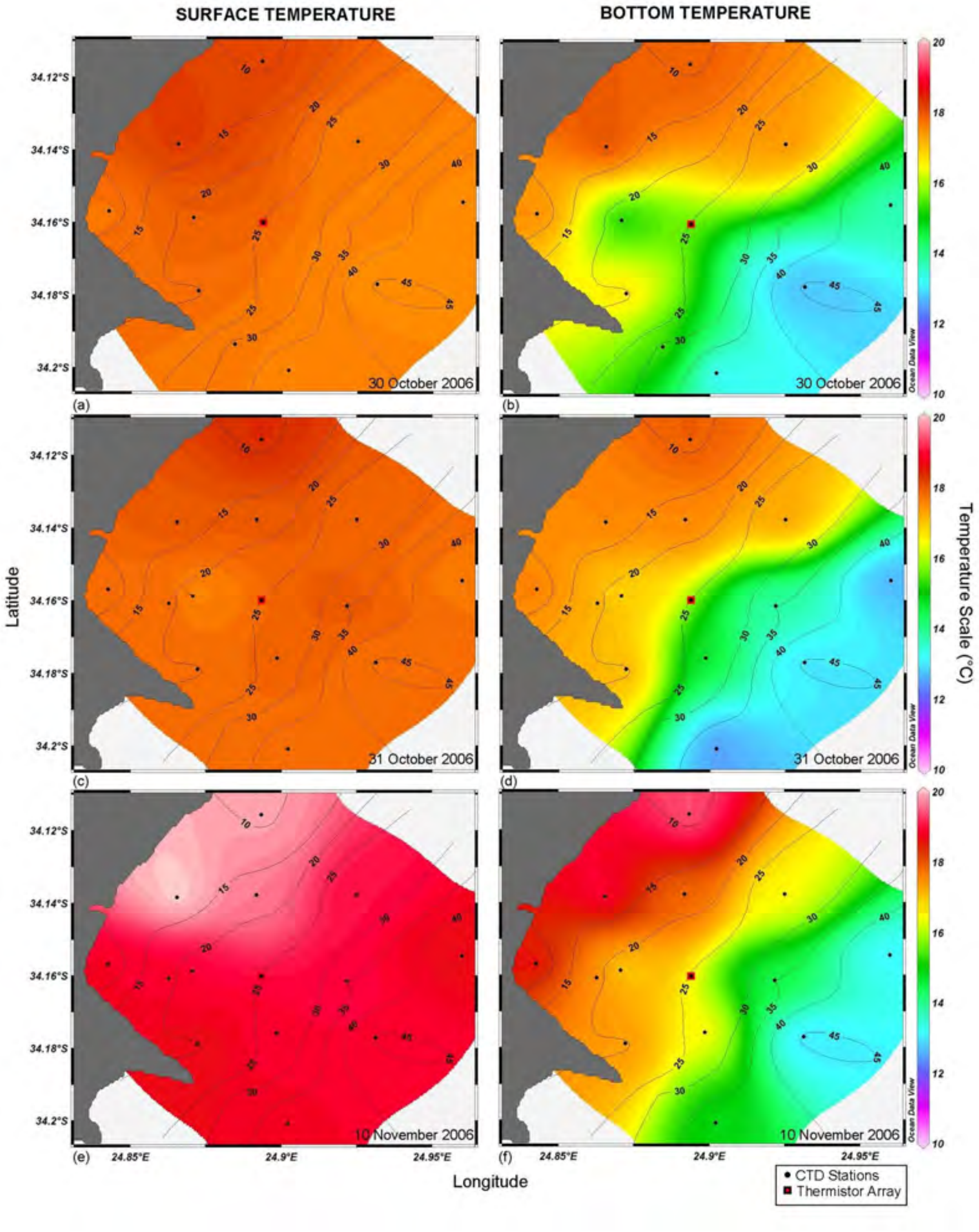


Figure 16: Surface and bottom temperatures, respectively, in Kromme Bay, on (a and b) the 30 October 2006, (c and d) 31 October 2006 and (e and f) the 10 November 2006. The contour lines depict bathymetry.

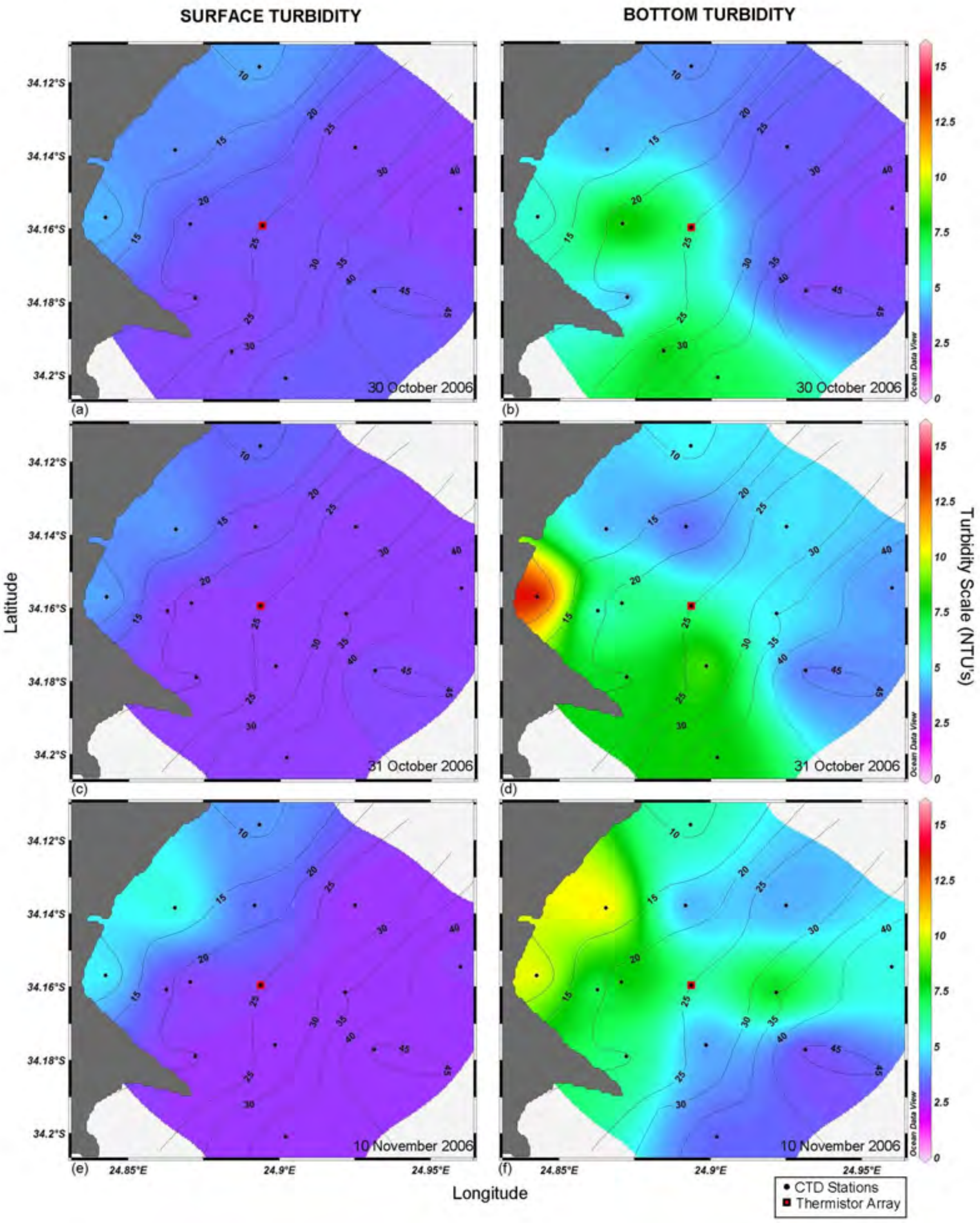


Figure 17: Surface and bottom turbidity, respectively, in Kromme Bay, on (a and b) the 30 October 2006, (c and d) the 31 October 2006 and (e and f) the 10 November 2006. The contour lines depict bathymetry.

In addition, due to the increased swell resulting from the strong westerly, turbidity levels at the Kromme River mouth (see Fig. 14) increased to ~25 NTU's and a turbid water mass (~65 NTU's) began moving into the bay (Fig. 20d). Surface turbidity remained low (~2.5 NTU's) (Fig. 20c). Prior to the strong southwesterly and the initiation of the turbidity event, surface and bottom turbidity levels were <4 NTU's (Fig. 20a and b).

Immediately evident in Fig. 21a, Fig. 22a and Fig. 23a was the similarity in bottom temperature between sites 1 and 2. However, upon closer examination (Fig. 21b, Fig. 22b and Fig. 23b) it became apparent bottom temperature at the shallower site 1 was generally warmer than at site 2. Temperatures at site 1 were warmer 87.9 % of the time, with a maximum temperature difference of 1.98 °C. Interestingly, when an upwelling event was recorded at site 2, a time lag existed before a drop in temperature was recorded at site 1. In some instances, temperatures at site 1 only equalled those at site 2 some 105 hours after the upwelling event was first recorded. On three occasions (27 July 2008 – Fig. 21b, 5 August 2008 – Fig. 21b and 25 October 2008 – Fig. 23b), bottom temperature at site 1 did not drop at all when a small scale upwelling event was recorded at site 2.

Another pattern evident was the occurrence of an upwelling event immediately after an easterly component wind (Fig. 21a and c, Fig. 22a and c and Fig. 23a and c). The stronger the wind and the greater the length of time the easterly wind dominated, the more extreme was the drop in temperature and the duration of the upwelling events longer. In those instances where a drop in temperature was only recorded at site 2 and not at site 1, a strong easterly wind of short duration was immediately followed by an equally strong or stronger westerly component wind (27 July 2008 – Fig. 21c, 5 August 2008 – Fig. 21c and 25 October 2008 – Fig. 23c).

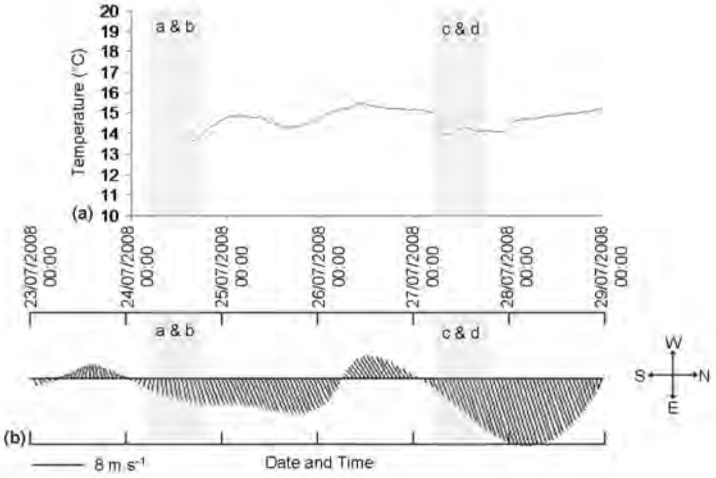


Figure 18: (a) Hourly bottom temperature recorded at the squid buoy during the small boat CTD survey in 2008 and (b) hourly wind data recorded at Port Elizabeth during the same time period. The shaded areas refer to the gridded ODV plots (a to d) in Fig. 19 and Fig. 20.

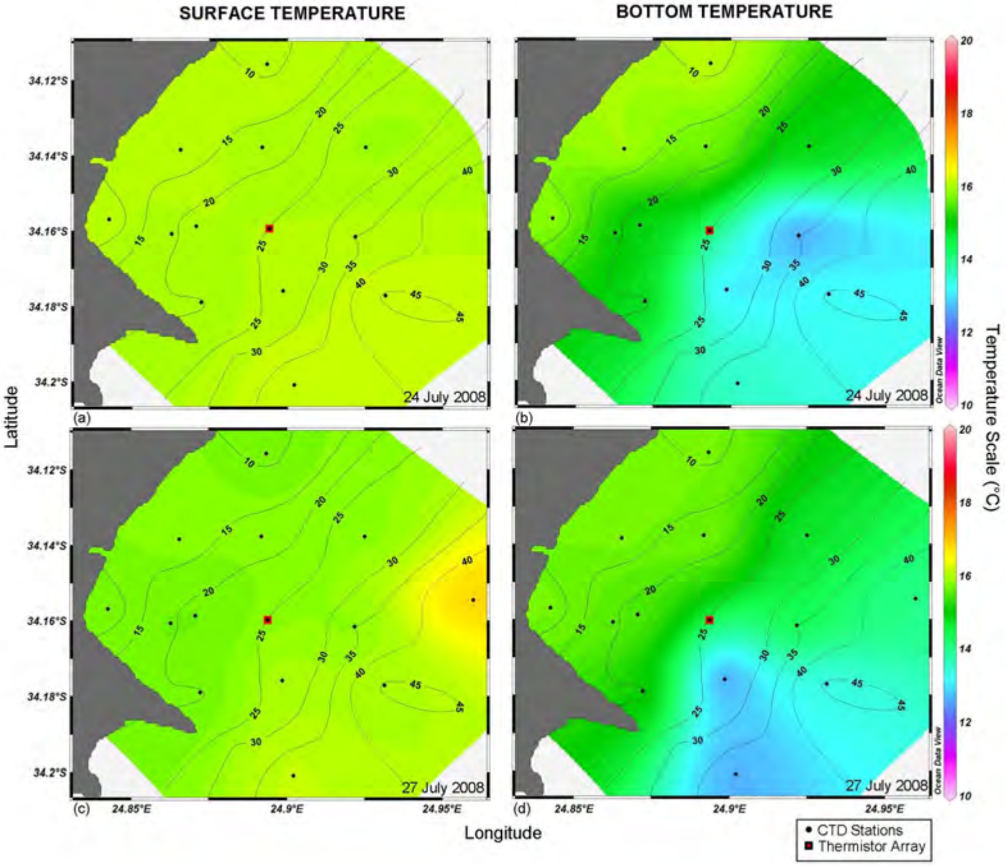


Figure 19: Surface and bottom temperatures, respectively, in Kromme Bay, on (a and b) the 24 July 2008 and (c and d) the 27 July 2008. The contour lines depict bathymetry.

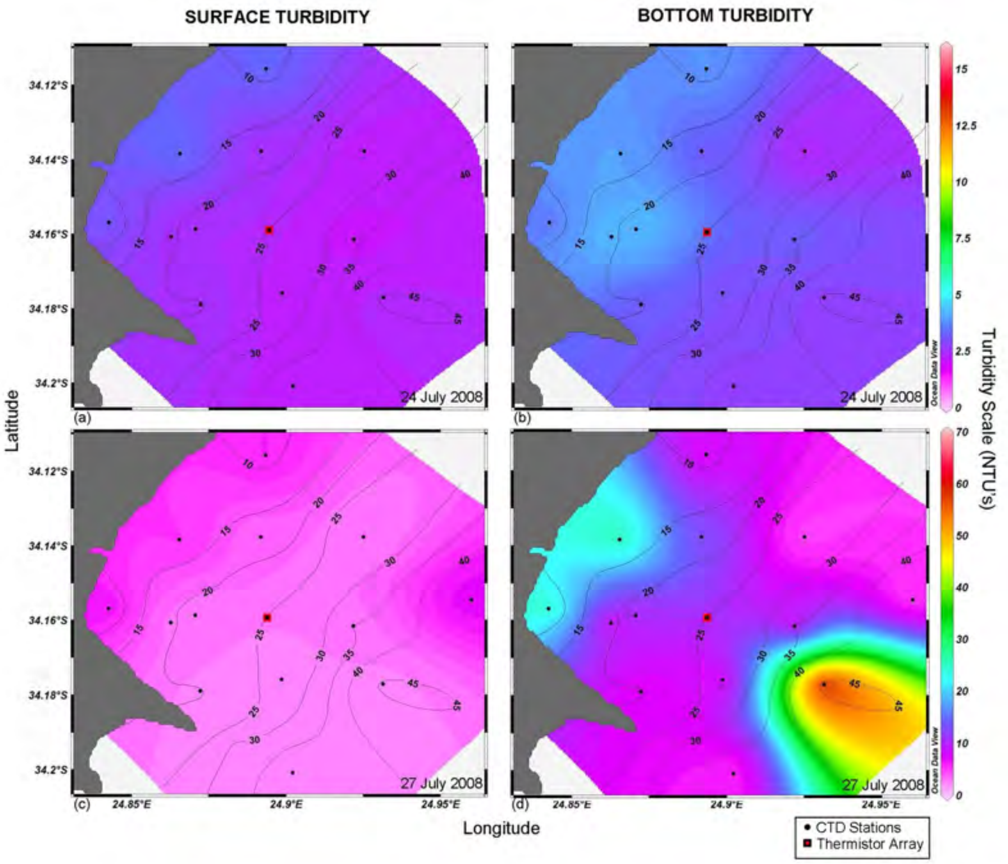


Figure 20: Surface and bottom turbidity, respectively, in Kromme Bay, on (a and b) the 24 July 2008 and (c and d) the 27 July 2008. The contour lines depict bathymetry.

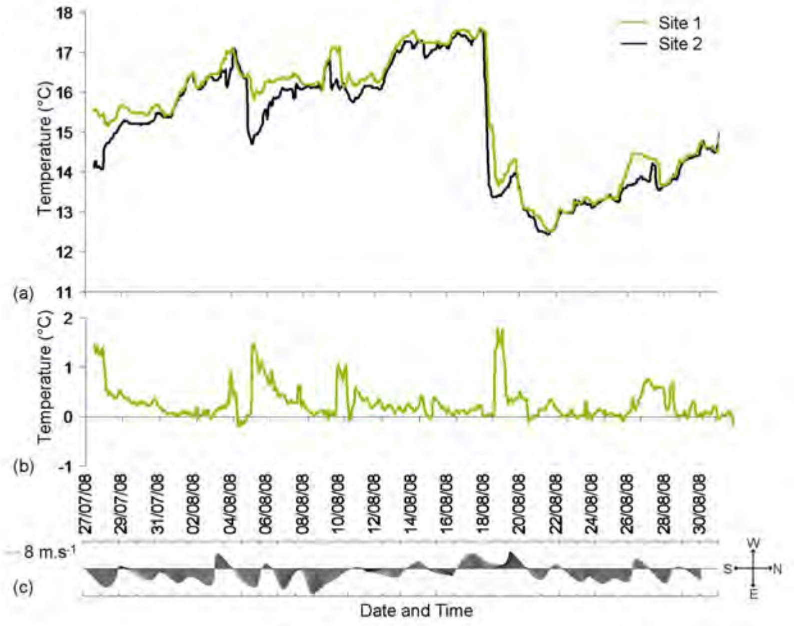


Figure 21: Comparison of bottom temperatures, from the 27 July 2008 to the 31 August 2008, at two different sites in Kromme Bay: the thermistor array (Site 2) and the additional UTR (Site 1) (Figure 14). Hourly bottom temperature data for (a) both sites and (b) the difference in temperature recorded at site 1 compared to that recorded at site 2 have been plotted. Also illustrated is (c) the relevant hourly wind data for the same time period.

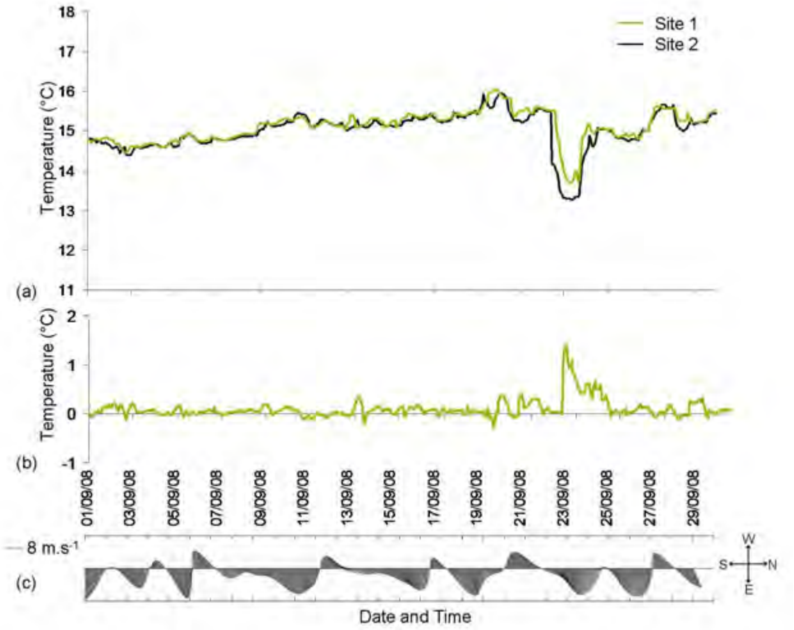


Figure 22: Comparison of bottom temperatures, from the 1 September 2008 to the 30 September 2008, at two different positions in Kromme Bay: the thermistor array (Site 2) and the additional UTR (Site 1) (Fig. 14). Hourly bottom temperature data for (a) both sites and (b) the difference in temperature recorded at site 1 compared to that recorded at site 2 have been plotted. Also illustrated is (c) the relevant hourly wind data for the same time period.

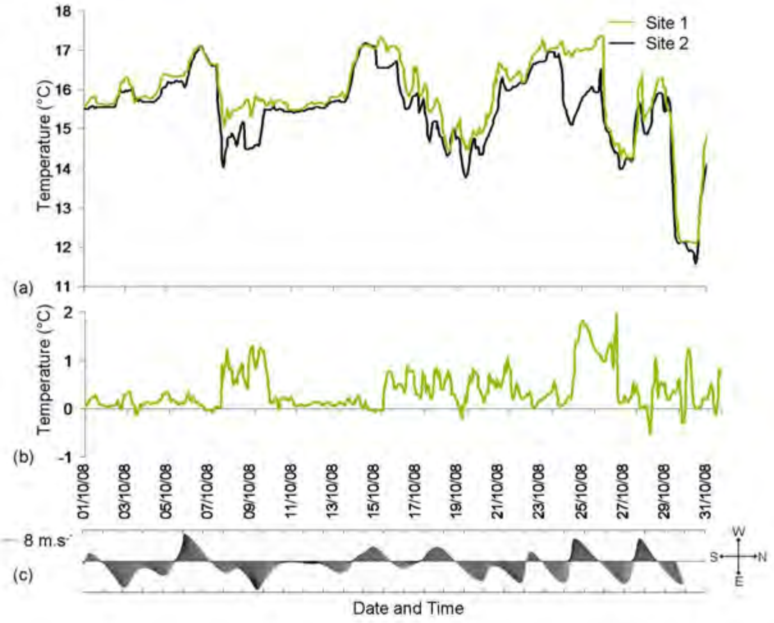


Figure 23: Comparison of bottom temperatures, from the 1 October 2008 to the 31 October 2008, at two different positions in Kromme Bay: the thermistor array (Site 2) and the additional UTR (Site 1) (Fig. 14). Hourly bottom temperature data for (a) both sites and (b) the difference in temperature recorded at site 1 compared to that recorded at site 2 have been plotted. Also illustrated is (c) the relevant hourly wind data for the same time period.

4.4. Discussion

A number of studies have shown the prominent headlands or capes along the south coast of South Africa to be areas where upwelling results from easterly component winds (Beckley 1983; Schumann *et al*. 1982; Schumann *et al*. 1988). Cold water upwelled on the southern shoreline of these capes then moves westwards (Goschen and Schumann 1995) and offshore as a consequence of the resulting upwelling alongshore current (Schumann 1999). Apart from moving westwards, upwelled water along the southern shoreline of a cape can also be advected around the point of the cape and into the bay formed by the northern shoreline (Goschen and Schumann 1995). Post-upwelling westerly or southwesterly winds can drive surface water away from the northern side of a cape (Goschen and Schumann 1995). The offshore-driven surface water would then be replaced from below by the upwelled water that was advected around the point of the cape by way of Kelvin waves (Goschen and Schumann 1995).

Cold upwelled water moving around Cape St Francis and into Kromme Bay in such a way would result in a drop in temperature at site 2, followed by a temperature drop at site 1 a number of hours later (Fig. 14). However, it appears that if the upwelling event is minor or of short duration and post-upwelling westerly winds strong, downwelling occurs and bottom waters can warm before reaching site 1 (Fig. 21 and Fig. 23). As a result, a certain degree of spatial variation in bottom temperature can occur within Kromme Bay.

The small boat CTD survey has also shown spatial variation to occur in turbidity levels within Kromme Bay (Fig. 17 and Fig. 20). Upwelling and downwelling results in the movement of turbid water masses up and down the seabed slope (Dorfler 2002). An upwelling event can result in turbid water moving into Kromme Bay. Dorfler (2002) however, found that often in these instances, bottom turbidity levels would decrease again before the lowest bottom temperature was reached. Dorfler (2002) showed the majority of inshore turbidity events to be a result of westerly winds causing downwelling and an increase in swell height. Turbid bottom waters then moved away from the inshore regions into deeper waters. As a result of riverine deposition of organic and inorganic matter, the benthic nephloid layer at the Kromme River mouth is probably quite dense compared to other areas of the bay. Increased swell would lift this nephloid layer, extending it into the water column. This would explain the higher turbidity levels in the vicinity of the Kromme River mouth during the small boat CTD surveys on the 31 October 2006 (Fig. 17d) and 10 November 2008 (Fig. 17f). Another turbid water mass was recorded on the 27 July 2008 (Fig. 20d), no doubt as a result of the increased swell due to strong westerly winds. Interestingly, once again, turbidity levels were highest in the vicinity of the Kromme River mouth in comparison to the middle of the bay. In this instance, high turbidity levels were also recorded just outside of Kromme Bay. This further illustrates the spatial variation in turbidity conditions that can occur within this bay. These turbidity events can persist for a number of days, extending in the water column as far as the thermocline (Dorfler 2002).

4.5. Conclusions

It can be concluded that environmental conditions recorded at the thermistor array site are not always indicative of conditions throughout the bay. From the bottom temperature comparison between site 1 and site 2, temperatures measured at site 2 can be said to be fairly similar to those experienced elsewhere in the bay, although there might be a slight difference in temperature and the time of onset of upwelling/downwelling events. It has been found however, that upwelling events of short duration may be reversed and not perpetuated throughout the bay as a result of strong post-upwelling westerly winds. Only in this instance would temperature measured at the thermistor array site be a poor indication of an upwelling event elsewhere in the bay. Turbidity levels recorded at the thermistor array site, appear to be a poor indication of conditions elsewhere in the bay. High turbidity levels were recorded near the Kromme River mouth, on the western side of the bay and just outside of the bay. In none of these instances would an OBS-3A suspended solids and turbidity monitor (Campbell Scientific) deployed at the thermistor array site have recorded the highest turbidity levels or the extent of the turbidity event. Similarly, a turbidity event recorded at the thermistor array site may not exist elsewhere in the bay.

CHAPTER 5

The effect of temperature and turbidity on spawning chokka squid *Loligo reynaudii*

5.1. Introduction

Hanlon *et al*. (1994) emphasized the importance of studying an animals' behaviour in its natural environment despite the difficulties. Unfortunately, diver observations on the chokka squid inshore spawning grounds are limited to approximately 30 to 40 minutes at one time (Hanlon *et al*. 1994). The use of underwater video extends observation time but still has limitations. Footage can only be recorded during daylight hours (the use of artificial lighting at night may disrupt the squids' natural behaviour) and during periods of good visibility. Unfortunately, turbidity events which reduce visibility, occur frequently on the inshore spawning grounds (Dorfler 2002).

Acoustic telemetry however, offers us a means of "observing" individual animals uninterrupted for long periods of time. Such systems have successfully been used to study migration/movements (Acolas *et al*. 2006; Acolas *et al*. 2004; Almeida 1996; Brill *et al*. 1995; Carr *et al*. 1997; Carr *et al*. 2004; Egli and Babcock 2004; Humston *et al*. 2005; Windle and Rose 2005), behaviour (Acolas *et al*. 2006; Acolas *et al*. 2004; Aitken *et al*. 2005; Cooke and Philipp 2004; Egli and Babcock 2004; Girard *et al*. 2004; Jadot *et al*. 2006; Løkkeborg *et al*. 2000; Mitamura *et al*. 2005; Robichaud and Rose 2003; Vabø *et al*. 2004), survival (Cooke and Philipp 2004; Welch *et al*. 2004), residency (Brooking *et al*. 2006; Humston *et al*. 2005; Robichaud and Rose 2003; Welch *et al*. 2004), habitat use (Brill *et al*. 1995; Brooking *et al*. 2006; Jadot *et al*. 2006) and home-range size (Jadot *et al*. 2006) in a variety of marine species. The type of system (i.e.: active or passive tracking system), the placement of stationary receivers and the type of transmitters used varies from study to study. It is dependent on the species being studied, the movement range of the animal, the size of the area being monitored and the aims of the research itself.

The research reported on in this chapter had two major aims: The first being to determine the direct effect of major upwelling and turbidity events on existing spawning aggregations and hence on catches. The second aim was to expand on the existing knowledge of spawning behaviour and movement on the spawning grounds. To achieve both these objectives, direct observations of spawning individuals was required. A passive acoustic telemetry system with stationary receivers was the chosen method for recording behavioural, presence-absence and depth data in this study. Findings from Chapter 3, which investigated the integrity of the receiver array used and its’ limitations, and findings from Chapter 4, which investigated the spatial variation of oceanographic conditions in Kromme Bay, were incorporated into the results.

5.2. Materials and Methods

Kromme Bay (St Francis Bay) was the chosen study site for four acoustic telemetry experiments conducted during the squid fishery closed seasons of November 2003, 2004, 2005 and 2006 (Fig. 24). Kromme Bay forms part of the main spawning grounds and various levels of fishing activity occur in this area throughout the year. For this reason, the closed fishing season was chosen to avoid impacts of boat anchors on instrumentation and intense commercial fishing on the spawning process.

5.2.1. Acoustic arrays

All acoustic telemetry equipment (stationary receivers and transmitters) was purchased from *Vemco*, Ltd. Nova Scotia, Canada. VR2 receivers were deployed in a hexagonal array (Fig. 13 and Fig. 14). This design allowed for the monitoring of an area up to 1.28 km^2, depending on thermal conditions of the water column (Chapter 3). The mooring design of individual VR2 receivers is given in Figure 25. Each VR2 receiver was deployed 5 m above the seabed using a hollow core polypropylene rope. A subsurface buoy was used to maintain tension on the rope and hence the position of the VR2 receiver in the water column. The mooring was anchored to the seabed using a 50 kg weight.

5.2.2. Tagging

Male and female squid were tagged with V9 acoustic transmitters (Fig. 26a). To allow for the attachment of transmitters to the squid, two 18-gauge hypodermic needles were glued to the surface of each transmitter (Fig. 26a). Hypodermic needle lengths varied depending on the sex and size of the animal tagged. Hypodermic needles with a length of 17 mm where used for large males and needles with a length of 14 mm used on smaller sneaker males and females. Squid were caught on active spawning sites, within the hexagonal array of VR2 receivers, using a jig. The animals were removed from the water, sexed and placed on a damp cloth (Fig. 27a). The transmitter was inserted (Fig. 27a) using an applicator designed specifically for use on chokka squid (Fig. 26b). The applicator was initially held sideways and slipped into the mantle cavity (Fig. 26b). The apparatus was turned through 90° and the protective applicator sheath removed (Fig. 26b), pushing the hypodermic needles through the mantle (Fig. 27b). Nylon washers were then pushed onto the hypodermic needle ends (Fig. 26c and Fig. 27c) and held in place with copper crimps (Fig. 26c and Fig. 27d and e). The squid were placed in a plastic bin alongside the boat, or simply held alongside the boat if sea conditions were too rough, to recover (Fig. 27f). Once the animal had resumed normal fin beating and swimming behaviour, it was released on the capture site.

The effect of the transmitters on squid was studied in detail by Rigby (2000). She noted behavioural changes after transmitter attachment. Behaviour did however stabilize and return to normal after a certain period of time. The time interval appeared to be dependent on the squid/transmitter weight ratio, resulting in the resumption of normal behaviour one day after tagging for males, two days for sneaker males and three days for females. Video footage, recorded during the current study however, showed that after release, tagged individuals immediately reintegrated back into the spawning aggregation and appeared to resume normal behaviour.

A total of 45 squid were tagged over the four experiments. Transmitters used in 2003 did not have pressure sensors and therefore only presence-absence data was collected. Transmitters with pressure sensors were used in 2004, 2005 and 2006, providing depth as well as presence-absence data. Duration, details of transmitters used, the total number of squid tagged and the number of males and females tagged per acoustic telemetry experiment are given in Table VIII. To correct possible time drift of individual VR2 receiver clocks, VR2 data files were time corrected using a program created by Dr. Dale Webber (*Vemco*). Data were analysed for presence-absence on the spawning site, vertical occupation of the water column and diurnal behaviour patterns.

5.2.3. Environmental monitoring

Temperature data were collected using Star-oddi Starmon mini underwater temperature recorders (UTR's) moored 50 m from the squid buoy (Fig. 6) at depths of 9, 14, 18, 21 and 24 m. This array of UTR's is referred to as the thermistor array. The UTR's were programmed to record temperature at hourly intervals. When sea conditions permitted, daily temperature, turbidity and salinity profiles at the squid buoy were obtained using a portable CTD (Seabird 19 Plus). In 2003 an OBS-3A suspended solids and turbidity monitor (Campbell Scientific) was also deployed on the thermistor array, 83 cm from the bottom. In 2005, an OBS-3A was deployed 83 cm from the bottom in the centre of the VR2 receiver array. The OBS-3A's were programmed to record turbidity levels at hourly intervals. No turbidity data was collected in 2006 due to the failure of equipment (OBS-3A and portable CTD). Port Elizabeth hourly wind data for the relevant periods was obtained from the South African Weather Services[XI]. A UNH Lanczos filter (weighted 73) was applied to the data and stick vector plots generated using ADCP Data Analysis Software (ADAS)[XII]. Wind direction is orientated away from the axis and not towards it.

[XI] South African Weather Service. 2003, 2004, 2005, 2006. Wind Data.

[XII] Duncan, L.; Duncan, F. and Nelson, G. ADCP Data Analysis Software. 1.3.1.43.

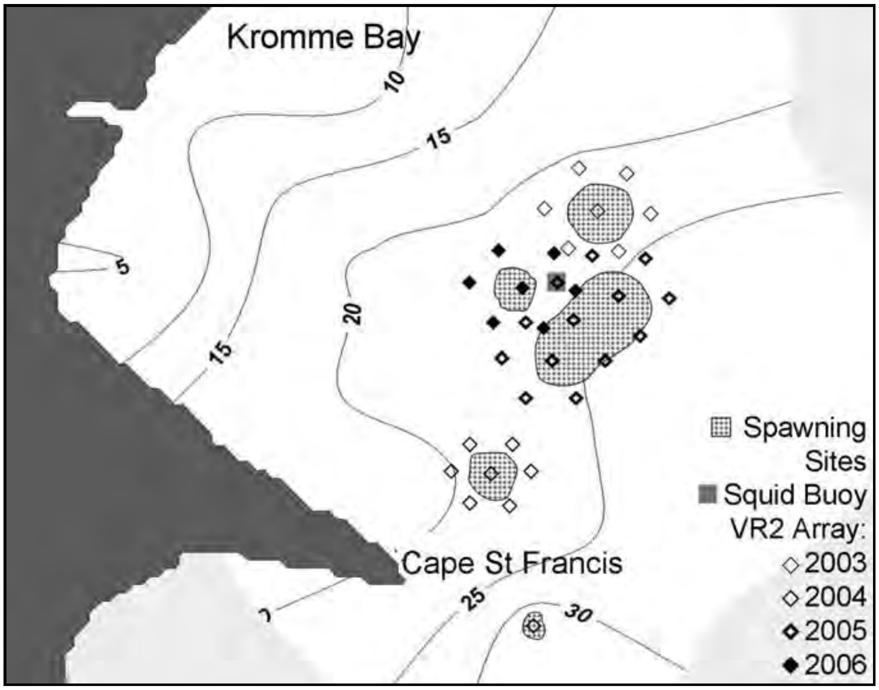


Figure 24: Diagram showing the study site, Kromme Bay, as well as the placement of the hexagonal VR2 receiver arrays for the years 2003, 2004, 2005 and 2006. Contour lines depict the bathymetry of Kromme Bay.

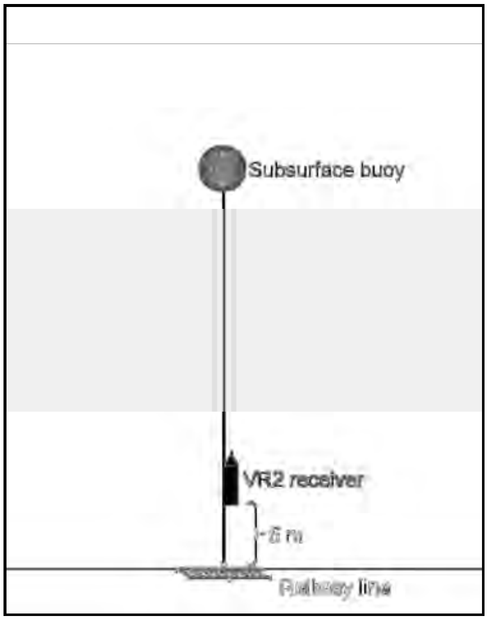


Figure 25: The mooring design for individual VR2 receivers.

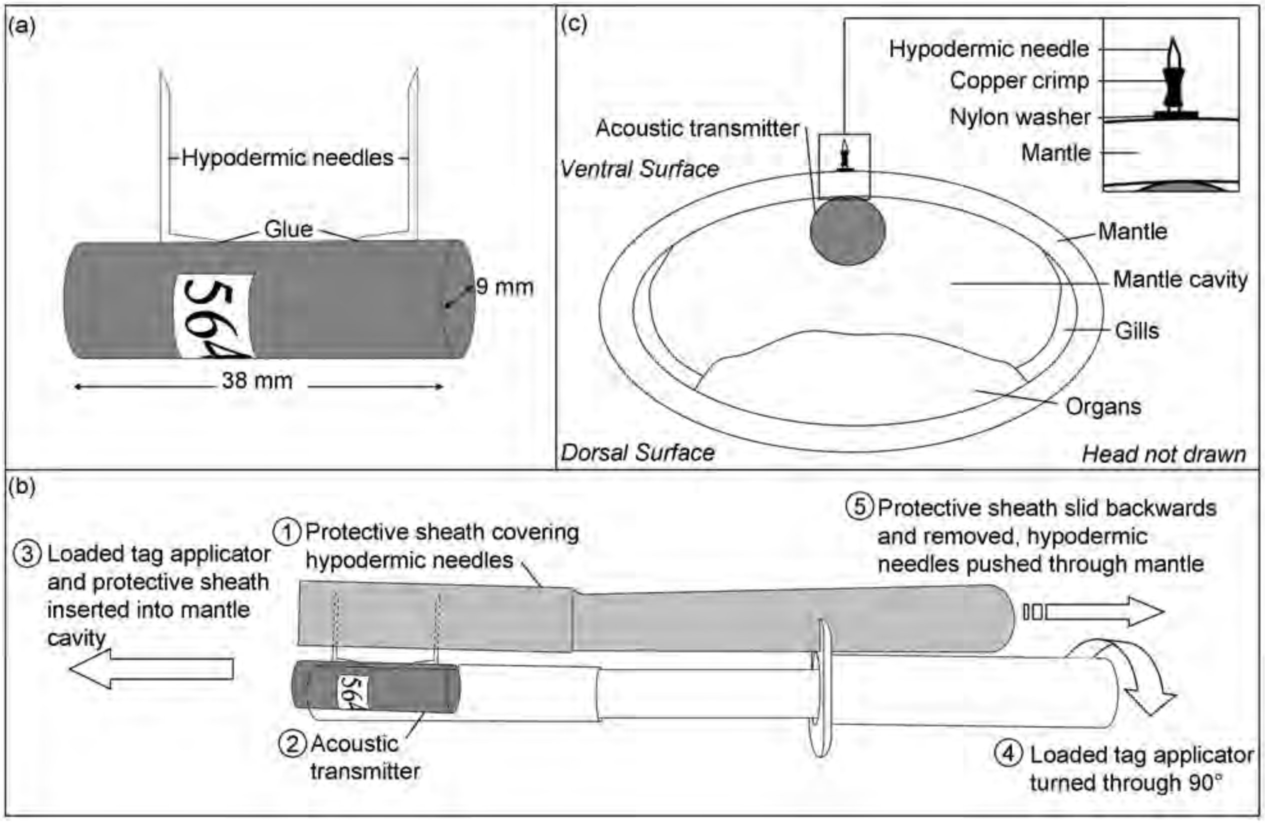


Figure 26: Instrumentation used for tagging. (a) The attachment of hypodermic needles to an acoustic transmitter, (b) the specially designed tag applicator used to acoustically tag *Loligo reynaudii* and (c) the placement of the acoustic transmitter within the mantle of the squid, on the ventral side, too avoid piercing organs with the hypodermic needles.

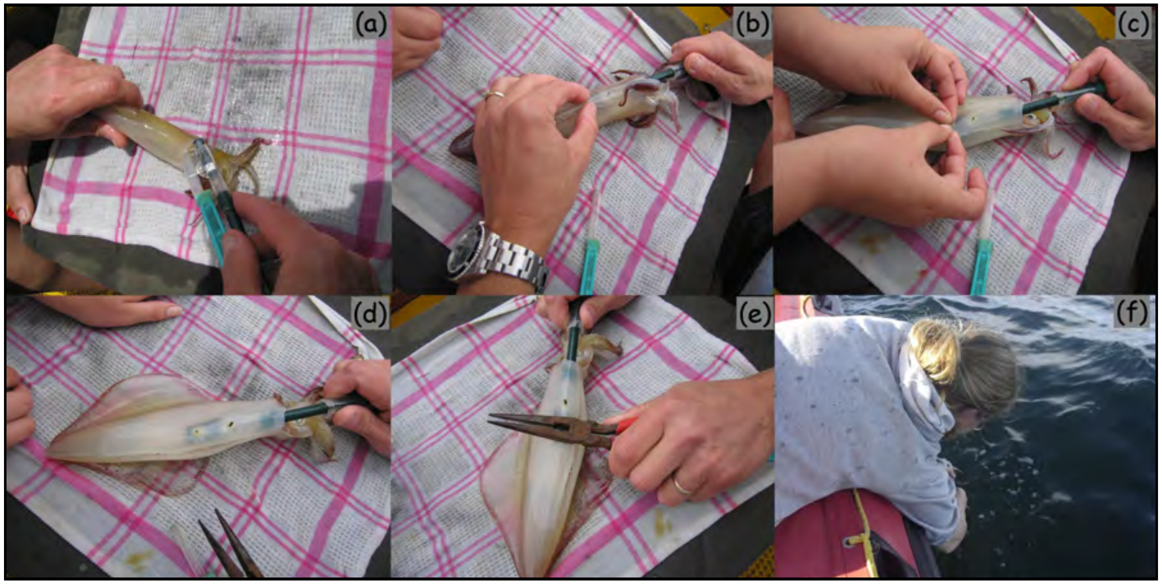


Figure 27: Attaching a transmitter to a squid: (a) A transmitter was inserted beneath the mantle using a specifically designed applicator. (b) The apparatus was turned through 90° and the protective applicator sheath removed, pushing the hypodermic needles through the mantle. (c) Nylon washers were then pushed onto the hypodermic needle ends and (d) a metal cylinder slipped over each hypodermic needle. (e) The metal cylinders were crimped using a long nose pliers. (f) The squid was held submerged alongside the boat until strong swimming ability was displayed (fin beating). Only then was the animal released on the capture site.

Table VIII: Duration, details of transmitters used and the number of squid tagged during acoustic telemetry experiments conducted in 2003 to 2006.

Year	Duration of acoustic telemetry experiment	Tag Type	Minimum off Time (s)	Maximum off Time (s)	Pressure Sensor	Number of Animals Tagged	Males	Females
2003	12 Nov-22 Nov	V8SC-2H-R256	10	35	No	4	2	2
2004	07 Nov-21 Nov	V9P-6L-S256	30	90	Yes	12	6	6
2005	14 Nov-21 Nov	V9P-6L-S256	20 30	69 90	Yes	23	13	10
2006	16 Nov-21 Nov	V9P-6L-S256	30	90	Yes	6	4	2

5.3. Results

5.3.1. Acoustic Telemetry Experiments

Well-established spawning aggregations were monitored in 2003, 2004 and 2005. The date and environmental conditions at formation were therefore unknown. In 2006, no squid were found within Kromme Bay until the formation of an aggregation around the 14/15 November (discovered 15 November). Interestingly, this aggregation formed after bottom temperature dropped from 16.5 °C to 11.5 °C (Figure 28).

Squid ID codes, tagging details and a summary of the data collected per individual squid are given in Table IX. Day has been taken as the period between 05:01 and 19:00 and night between 19:01 and 05:00.

5.3.2. Presence-absence on Spawning Sites

For each year all occurrences of the individual transmitters were plotted against date and time (Fig. 29 to Fig. 32). Bottom temperature and turbidity data over time were superimposed. Hourly wind data for each study period, measured at Port Elizabeth, has also been plotted in these figures. The number of hours each individual was present on the monitored spawning site, expressed as a percentage of the total number of hours of passive tracking (VR2 receivers), was calculated for each experiment (Table X). Also given in Table X is the percentage of time spent on the monitored spawning site per sex each experiment and also by all the tagged individuals per experiment. The percentage of tagged animals present over time for each experiment has been plotted in Figure 33. Hourly bottom temperature data has also been plotted.

In 2003 both male squid (M1 and M2) remained on the spawning site for a number of days and nights immediately after tagging (Fig. 29a). The females' (F1 and F2) presence was more sporadic but overall followed a pattern of being present during the day and leaving the spawning site shortly after sunset. M1 was present on the spawning site (30 %) for the longest period of time (Table X). M2 and F1 spent similar amounts of time in the vicinity of the egg bed (20 % and 21 % respectively), although these individuals were present at different times during the study. On average, males were present more often than females (25 %). It appears spawning intensity decreased as time progressed (Fig. 33a). However, only four animals were tagged in 2003 and a maximum number of two tagged individuals present at one time.

In 2004 the presence of tagged males and females appeared to be more erratic (Fig. 30a). Both males (M5, M6, M7, M8) and females (F3, F4, F5, F6, F7, F8) were present more often during daylight hours. Only one individual (F7) was continuously present, for a number of days (~60 hours). This animal also spent the most time on the spawning site (16 %), followed by F4 and F3 (15 % and 14 % respectively), compared to the other tagged individuals (Table X). On average females were present 8 % of the time, whereas males were only present for 5 % of the study period. Spawning intensity, indicated by the percentage of tagged animals present at any given time (Fig. 33b, n=12), decreased notably after the drop in bottom temperature on the 12 November 2004. Four squid (M4, M6, M7 and F4) were briefly detected by the VR2 receiver moored off Cape St Francis (indicated by the grey squares in Fig. 30a).

In 2005 the general presence-absence pattern was similar to that found in 2004. Males were present for long continuous periods compared to females (Fig. 31a and b). Females appeared to leave the spawning site more often. Again, the periods of absence usually occurred during the night. During this study, males on average spent more time on the spawning site compared to females (42 % and 34 % respectively) (Table X). M9, M12 and M10 were present for 86 %, 86 % and 83 %, respectively, of the total study period, the highest values compared to all tagged individuals. F14 and F11 also spent a great deal of time on the spawning site (66 % and 63 % respectively), compared to other individuals. Spawning intensity remained relatively high throughout the 2005 study (Fig. 33c, n=23).

Table IX: Squid ID codes, date of tagging, date of last detection, hours spent on the spawning site and the number of detections recorded for the 45 squid tagged in 2003, 2004, 2005 and 2006. Also shown in the table are means and standard deviations for each year and for all years combined.

Year and Squid Code	Sex	Date Tagged	Date of Last Detection	Time Spent on Spawning Site (hours)			Detections Recorded (%)		Total Number of Detections Recorded
				Day	Night	Total	Day	Night	
2003									
M1	Male	12/11	15/11	43	30	73	58 %	42 %	3 899
M2	Male	12/11	15/11	30	17	47	73 %	27 %	1 921
F1	Female	15/11	22/11	26	24	50	53 %	47 %	327
F2	Female	15/11	21/11	2	3	5	33 %	67 %	33
			mean ± s.d.	25.3 ± 17.1	18.5 ± 11.6	43.8 ± 28.3	54.3 % ± 16.3 %	45.7 % ± 16.3 %	1 545 ± 1 775
2004									
SM3	Sneaker male	07/11	08/11	3	10	13	30 %	70 %	40
M4	Male	07/11	11/11	7	7	14	51 %	49 %	91
M5	Male	07/11	08/11	13	2	15	96 %	4 %	294
M6	Male	08/11	20/11	38	4	42	97 %	3 %	721
M7	Male	08/11	09/11	8	2	10	95 %	5 %	185
M8	Male	08/11	08/11	2	0	2	100 %		29
F3	Female	07/11	12/11	31	15	46	52 %	48 %	814
F4	Female	07/11	10/11	37	12	49	78 %	22 %	1 167
F5	Female	09/11	09/11	3	0	3	100 %		71
F6	Female	09/11	09/11	5	5	10	67 %	33 %	109
F7	Female	09/11	11/11	31	22	53	56 %	44 %	1 412
F8	Female	09/11	09/11	2	0	2	100 %		31
			mean ± s.d.	15 ± 14.7	6.6 ± 6.9	21.6 ± 19.8	76.7 % ± 24.7 %	31.1 % ± 23.9 %	413.7 ± 489.3
2005									
M9	Male	14/11	21/11	101	44	145	74 %	26 %	3 668
M10	Male	14/11	21/11	96	43	139	67 %	33 %	2 918
M11	Male	14/11	21/11	71	10	81	91 %	9 %	1 646
M12	Male	15/11	21/11	95	50	145	64 %	36 %	3 453
M13	Male	16/11	21/11	14	0	14	100 %		165
M14	Male	16/11	21/11	39	14	53	58 %	42 %	640
M15	Male	17/11	21/11	58	15	73	82 %	18 %	1 298 (511-depth)
M16	Male	17/11	21/11	61	23	84	67 %	33 %	1613
M17	Male	19/11	21/11	21	3	24	86 %	14 %	579 (158-depth)
M18	Male	19/11	21/11	23	7	30	51 %	49 %	345

Year and Squid Codes	Sex	Date Tagged	Date of Last Detection	Time Spent on Spawning Site (hours)			Detections Recorded (%)		Total Number of Detections Recorded (n)
				Day	Night	Total	Day	Night	
2005 cont.									
M19	Male	19/11	21/11	15	2	17	99 %	1 %	156
M20	Male	19/11	21/11	36	20	56	51 %	49 %	745
SM21	Sneaker male	14/11	18/11	32	33	65	54 %	46 %	1 877
F9	Female	16/11	16/11	2	0	2	100 %		50
F10	Female	14/11	21/11	47	40	87	55 %	45 %	982
F11	Female	14/11	21/11	78	27	105	68 %	32 %	2 650
F12	Female	15/11	21/11	23	14	37	75 %	25 %	434
F13	Female	15/11	19/11	33	12	45	78 %	22 %	978
F14	Female	15/11	21/11	72	39	111	62 %	38 %	2 314
F15	Female	16/11	17/11	22	13	35	76 %	24 %	863
F16	Female	17/11	21/11	63	9	72	91 %	9 %	1 424
F17	Female	19/11	21/11	27	18	45	55 %	45 %	605 (175-depth)
F18	Female	19/11	21/11	30	7	37	87 %	13 %	629 (157-depth)
			mean ± s.d.	46 ± 28.8	19.3 ± 15.3	65.3 ± 41.8	73.5 % ± 16.2 %	29 % ± 14.6 %	1 305.7 ± 1 059.4
2006									
M22	Male	16/11	18/11	27	10	37	79 %	21 %	489
SM23	Sneaker male	17/11	20/11	20	11	31	76 %	24 %	403
SM24	Sneaker male	17/11	21/11	12	7	19	80 %	20 %	209
SM25	Sneaker male	17/11	21/11	8	6	14	44 %	56 %	130
F19	Female	16/11	17/11	5	4	9	43 %	57 %	54
F20	Female	16/11	17/11	7	2	9	88 %	12 %	58
			mean ± s.d.	13.2 ± 8.6	6.7 ± 3.4	19.8 ± 11.7	68.1 % ± 19.8 %	31.9 % ± 19.8 %	223.8 ± 183.2
		All years	mean ± s.d.	31.5 ± 27	14.1 ± 13.4	45.7 ± 38.6	71.9 % ± 19.6 %	31.6 % ± 17.9 %	944.9 ± 1 043.2

Presence on the monitored spawning site in 2006 was far less intense with again only two individuals, M22 and SM23, being present for long continuous periods (Fig. 32a). These two individuals spent the most time on the spawning site compared to the other four tagged animals (31 % and 26 % respectively) (Table X). These other individuals (SM24, SM25, F19 and F20) spent only short periods on the spawning site, most often during the day. As in 2003 and 2005, males were on average more often present on the spawning site compared to females (21 % and 8 % respectively) (Table X). Spawning intensity decreased noticeably from the 18 - 21 November 2006 (Fig. 33d).

Bottom temperature data indicated major upwelling events as a result of easterly winds during the experiments in 2003 (Fig. 29), 2004 (Fig. 30) and 2005 (Fig. 31). During these upwelling events surface and bottom temperatures differed by up to 7 °C, indicating intense thermoclines. In 2006 (Fig. 32) bottom temperatures remained relatively cold, fluctuating between 11 °C and 15 °C. The upwelling event in 2003 was rapid and of short duration, lasting ~24 hours (Fig. 29). Both males (M1 and M2) remained on the spawning site during the upwelling event recorded at the thermistor array site. During this time, both males were detected by all seven VR2 receivers (see Appendix A1), indicating considerable movement around the spawning site. As bottom temperatures at the thermistor array site increased again, M2 left the spawning site whereas M1 remained for another ~24 hours. For the rest of the 2003 study period, during which there was hardly any thermal stratification, only the female squid (F1 and F2) were present, albeit sporadically. In 2004 (Fig. 30), those tagged individuals (M4, F3 and F7) present on the spawning site as upwelling occurred immediately moved off. Again, this upwelling event had a rapid onset, but unlike the upwelling in 2003, it lasted a number of days. Squid presence was most intense before the upwelling event when bottom and surface temperatures were similar. For the remainder of this study period only one individual (M6) returned to the spawning site. Presence-absence data for 2005 (Fig. 31) showed squid presence to be intense as bottom temperatures gradually warmed and then cooled again. Bottom temperatures remained cold in 2006 and the presence of tagged individuals was sporadic.

Turbidity levels remained low in 2004 (<26 NTU's) (Fig. 30a) and 2005 (<8 NTU's) (Fig. 31a and b) and therefore cannot be considered a major factor influencing the behaviour of tagged individuals. However, a major turbidity event was recorded at the thermistor array site in 2003, immediately after the sudden and short upwelling event (Fig. 29). Bottom turbidity levels peaked at ~190 NTU's and turbidity levels remained high for 4.5 days during which time all tagged individuals (M1, M2, F1 and F2) were present (Fig. 29a). M2 and F2 seemed to pass through the spawning site whereas M1 and F1 remained in the area for a number of hours during the turbidity event recorded at the thermistor array site. No turbidity data was collected in 2006.

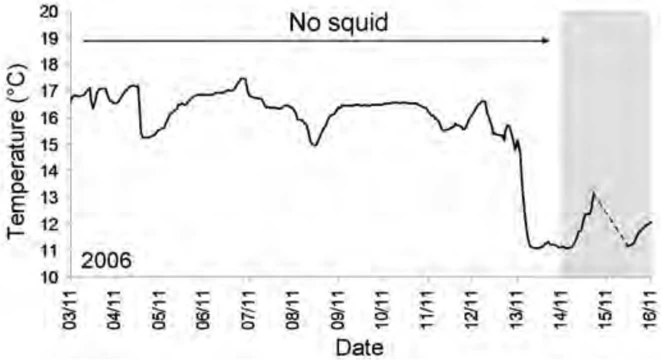


Figure 28: Temperature conditions before and during the formation of a spawning aggregation (shaded block) in 2006. The dashed line indicates a period during which no temperature data was recorded. Aggregations studied in 2003, 2004 and 2005 were already well-established upon discovery.

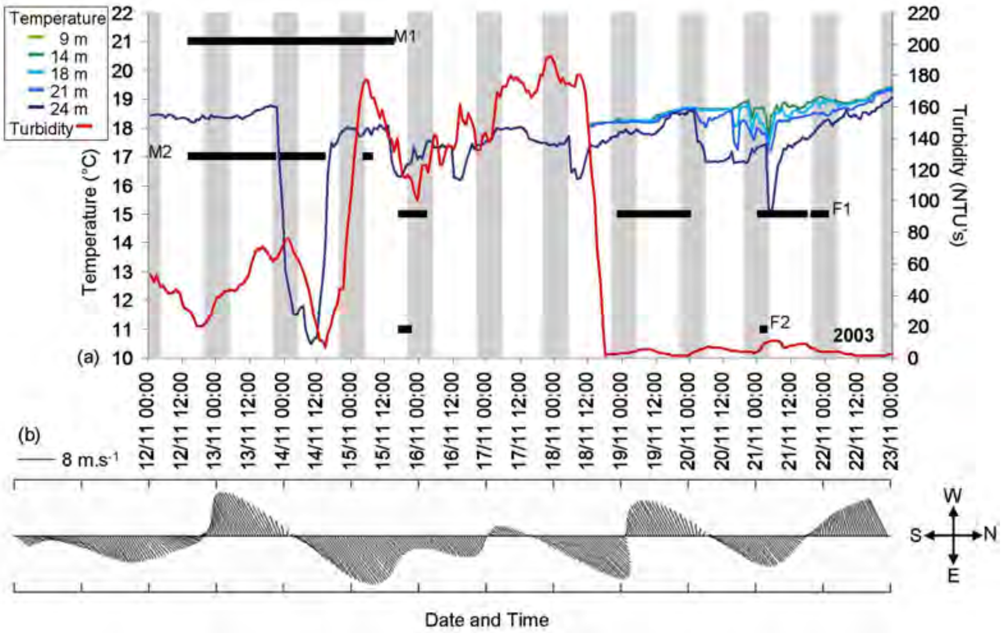


Figure 29: The (a) presence of individual tagged squid (indicated by a black square) on the monitored spawning site in 2003. Also illustrated are hourly temperature data for depths 14, 18, 21 and 24 m, hourly bottom turbidity data recorded using an OBS-3A, and (b) hourly wind data. Day/night periods are indicated by shaded areas.

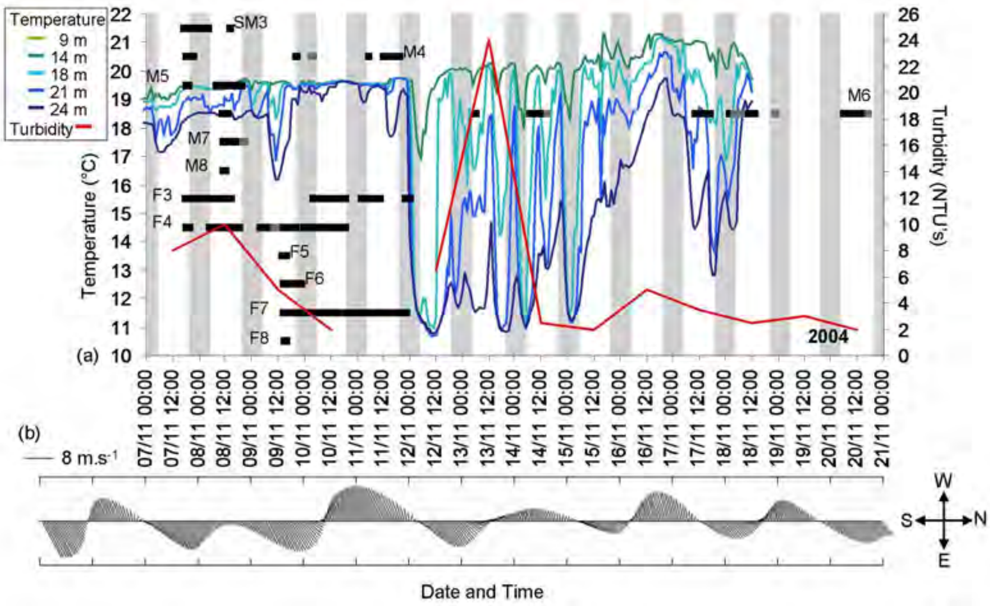


Figure 30: The (a) presence of individual tagged squid (indicated by a black square) on the monitored spawning site in 2004 (Grey squares indicate the presence of squid on the second deeper spawning site monitored). Also illustrated are hourly temperature data for depths 14, 18, 21 and 24 m, daily bottom turbidity data recorded using portable CTD and (b) hourly wind data. Day/night periods are indicated by shaded areas.

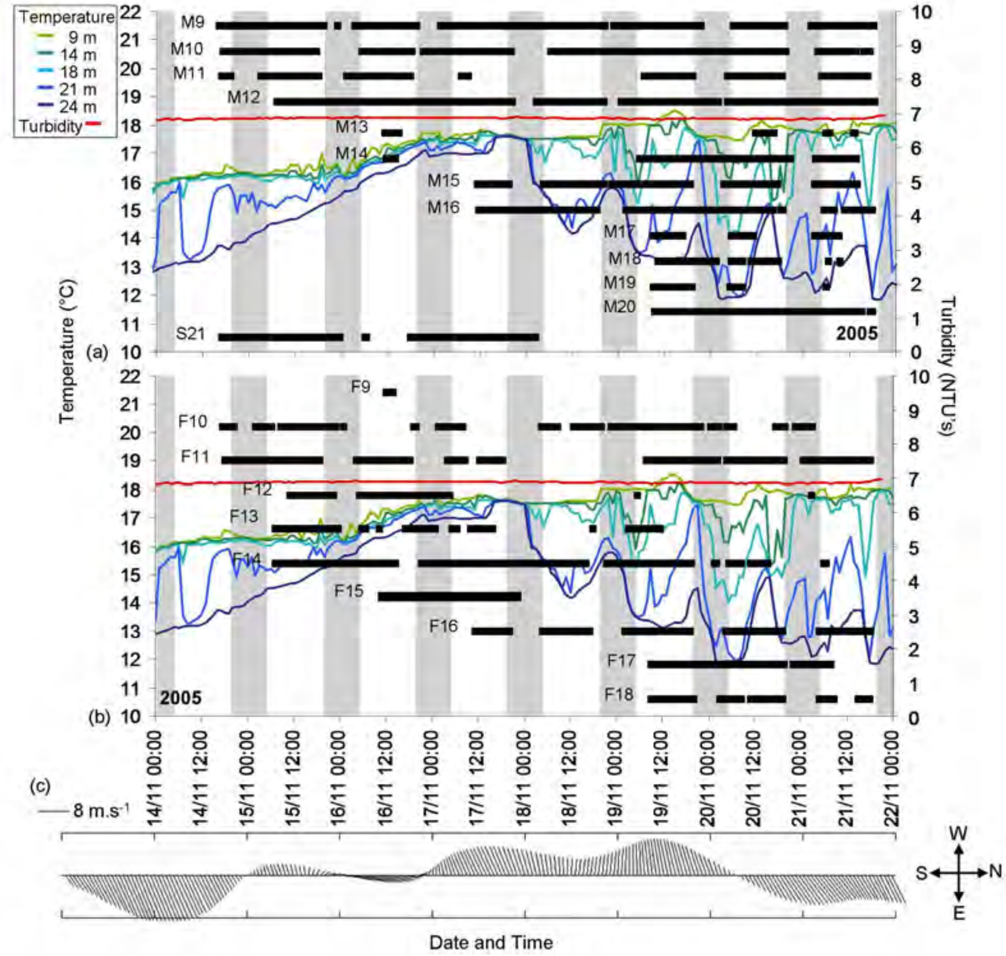


Figure 31: The presence of individual tagged (a) male and (b) female squid (indicated by a black square) on the monitored spawning site in 2005. Also illustrated are hourly temperature data for depths 9, 14, 18, 21 and 24 m, hourly bottom turbidity data recorded using an OBS-3A and (c) hourly wind data. Day/night periods are indicated by shaded areas.

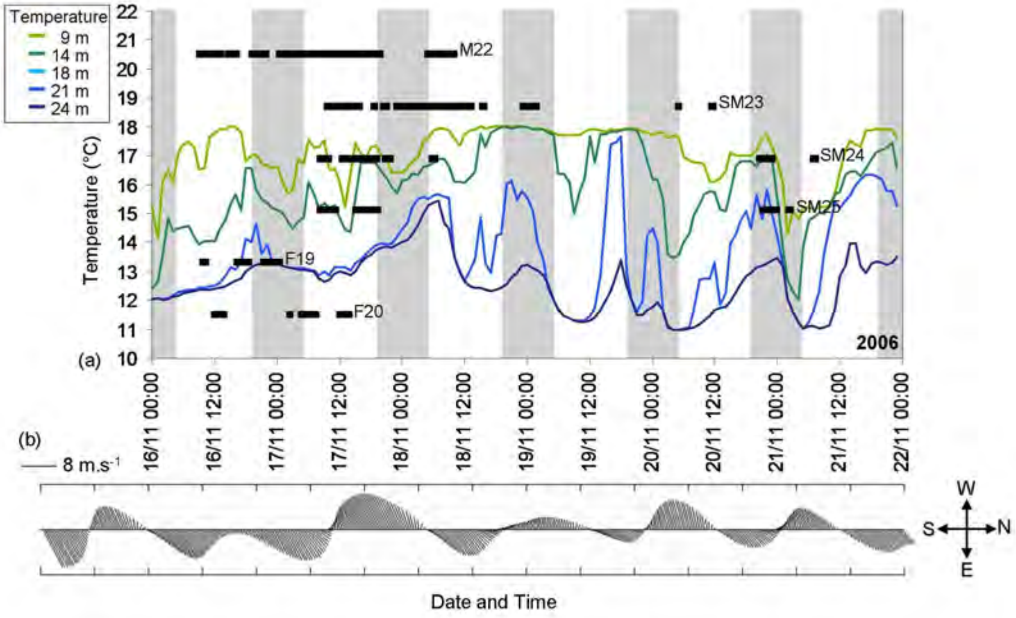


Figure 32: The (a) presence of individual tagged squid (indicated by a black square) on the monitored spawning site in 2006. Also illustrated are hourly temperature data for depths 9, 14, 21 and 24 m and (b) hourly wind data. Day/night periods are indicated by shaded areas.

Table X: The percentage of time spent on the monitored sites per individual, the average per sex and the average per experiment.

	Male			Female			
	Per Individual		Per Sex	Per Individual		Per Sex	Per Experiment
2003	M1	30%	25%	F1	21%	11%	18%
	M2	20%		F2	2%		
2004	SM3	4%	5%	F3	14%	8%	6%
	M4	4%		F4	15%		
	M5	4%		F5	1%		
	M6	13%		F6	3%		
	M7	3%		F7	16%		
	M8	1%		F8	1%		
2005	M9	86%	42%	F9	1%	34%	39%
	M10	83%		F10	52%		
	M11	48%		F11	63%		
	M12	86%		F12	22%		
	M13	8%		F13	27%		
	M14	32%		F14	66%		
	M15	43%		F15	21%		
	M16	50%		F16	43%		
	M17	14%		F17	27%		
	M18	18%		F18	22%		
	M19	10%					
	M20	33%					
	SM21	39%					
2006	M22	31%	21%	F19	8%	8%	17%
	SM23	26%		F20	8%		
	SM24	16%					
	SM25	12%					

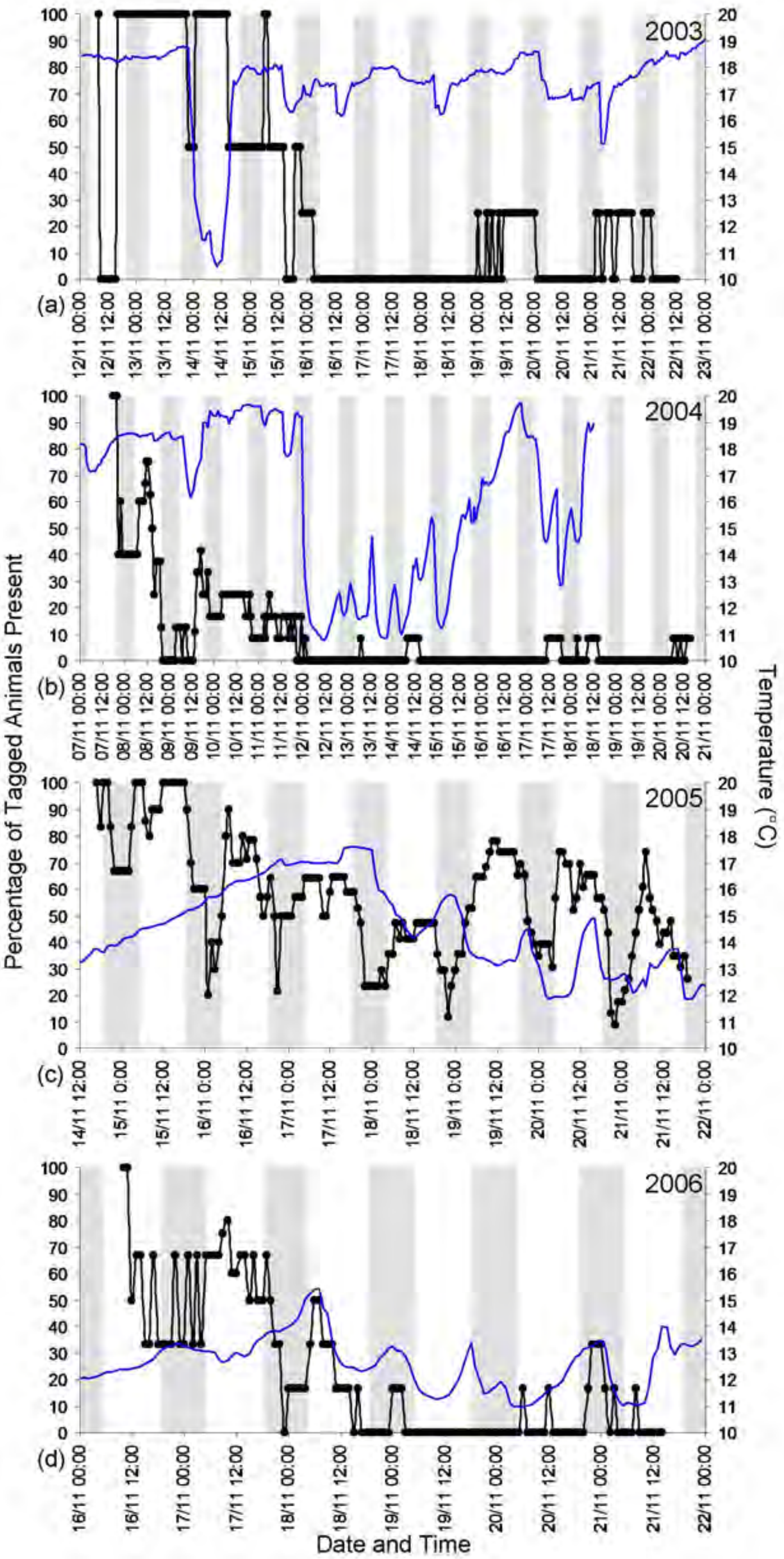


Figure 33: The percentage of tagged animals present over time for the years (a) 2003, (b) 2004, (c) 2005 and (d) 2006. Also shown is hourly bottom temperature (blue line) and day/night periods (night indicated by shaded areas).

5.3.3. Water Column Activity

Depth data for all male and female squid tagged in 2004, 2005 and 2006 are presented in Figure 34. As more than one receiver was deployed on the study site, duplicate data (i.e. single detections that had been recorded by more than one VR2 receiver) were removed for statistical purposes and the total number of successfully detected transmissions for each sex per day and night was calculated. The data for each sex was then separated into depth categories and the percentage of detections recorded in each depth category during the day and night plotted in Figure 35. Two sample, two-tailed t-tests were used to determine significant differences in mean depth during the day versus night for male, female and all squid combined as well as mean depth for males versus females during the day and night (Table XI). Bottom temperatures were superimposed in Figure 34.

It appears spawning, inferred by the upward-downward vertical movement close to the seabed evident in Figure 34, occurred at various temperatures. Mating and spawning behaviour is seen in a temperature range of 11.5 °C to 19.6 °C in the 2004 study (Fig. 34a and b), 11.8 °C to 17.6 °C in the 2005 study (Fig. 34c and d) and 12.3 °C to 15.4 °C in the 2006 study (Fig. 34e and f).

Figure 34a and b shows a sudden departure of squid from the spawning site as upwelling occurred in 2004. This upwelling event, resulting from strong easterly component winds, was sudden and bottom temperatures dropped rapidly by 0.7 $°C.hr^{-1}$. Prior to this upwelling event, squid present appeared to be spawning. The upwelling event occurring in 2005 was far more gradual and bottom temperatures cooled by 0.18 $°C.hr^{-1}$ (Fig. 34c and d). The intense pattern of spawning activity evident in both male and female plots (Fig. 34c and d) prior to this event continued uninterrupted throughout the onset of upwelling and during the upwelling event. In 2006 the recurrent warming and cooling of bottom waters was also relatively gradual (Fig. 34e and f), with no temperature change occurring at a rate faster than 0.14 $°C.hr^{-1}$. Spawning activity however was only evident during the first three days of this study (Fig. 34e and f). Individuals present after the 18 November 2006 were higher up in the water column and did not appear to be spawning.

Another pattern immediately evident in the depth plots is the diurnal vertical movement in the water column (Fig. 34). Both male and female squid moved higher up in the water column at night with males on occasion almost reaching the surface. During the day, activity was generally in close proximity to the seabed. This daily vertical migration is observable in all three years (2004, 2005 and 2006) pressure data was collected.

Table XI gives the results of two sample, two-tailed t-tests. Significant differences between the mean depth during the day and mean depth at night were found for all three groups (males, females and all squid combined) in the years 2005 and 2006, with the average depth during the day being deeper than that at night (Table XIa). Mean depths for the different periods in the day (day and night) were also compared between the sexes (Table XIb). Significant differences were found in all three years. In 2004 there was a significant difference in the mean depth of male and female squid during the day with female mean depth being only slightly deeper than that of males. No significant difference existed for mean depths at night. In 2005, during both the day and night, females had a significantly deeper mean depth than males. Mean depths for female squid during the day in 2006 were also significantly deeper than male mean depth although the degree of significance was not as great as that for during the night. The reverse was true for mean depths at night.

In 2004 both males and females had over 80 % of detections recorded in the depth category 20.1-25.0 m during the day (Fig. 35a and b). Tagged males and females did however differ in that during the day females occurred in depth categories throughout the water column, albeit at low frequencies. Males only occupied the depth categories between 15 and 30 m. At night females had the highest frequency of occurrence (~80 %) in the same depth category as during the day. Males were found to occur at low frequencies throughout the depth categories but mainly occupied the depth ranges 15.1-30.0 m. In 2005 both males and females (Fig. 35c and d) again had the highest frequency of occurrence in the same depth category (20.1-25.0 m) during the day. Females were again found to occur higher up in the water column than males during the day. At night males were most frequent in depth categories slightly shallower than females with the highest frequencies being at 10.1-15.0 m for males and 15.1-25.0 m for females. In 2006 the highest percentage of occurrence (~60 %) for males during the day was in the depth category 20.1-25.0 m (Fig. 35e). At night males were most frequent in the depth range 15.1-20.0 m. For the two female squid tagged however (Fig. 35f), patterns identified in 2004 and 2005 were not evident, possibly due to the low number of female squid tagged. The highest frequency of occurrence for females during the day was 40 % in the depth category 15.1-20.0 m and ~60 % at 5.1-10.0 m at night.

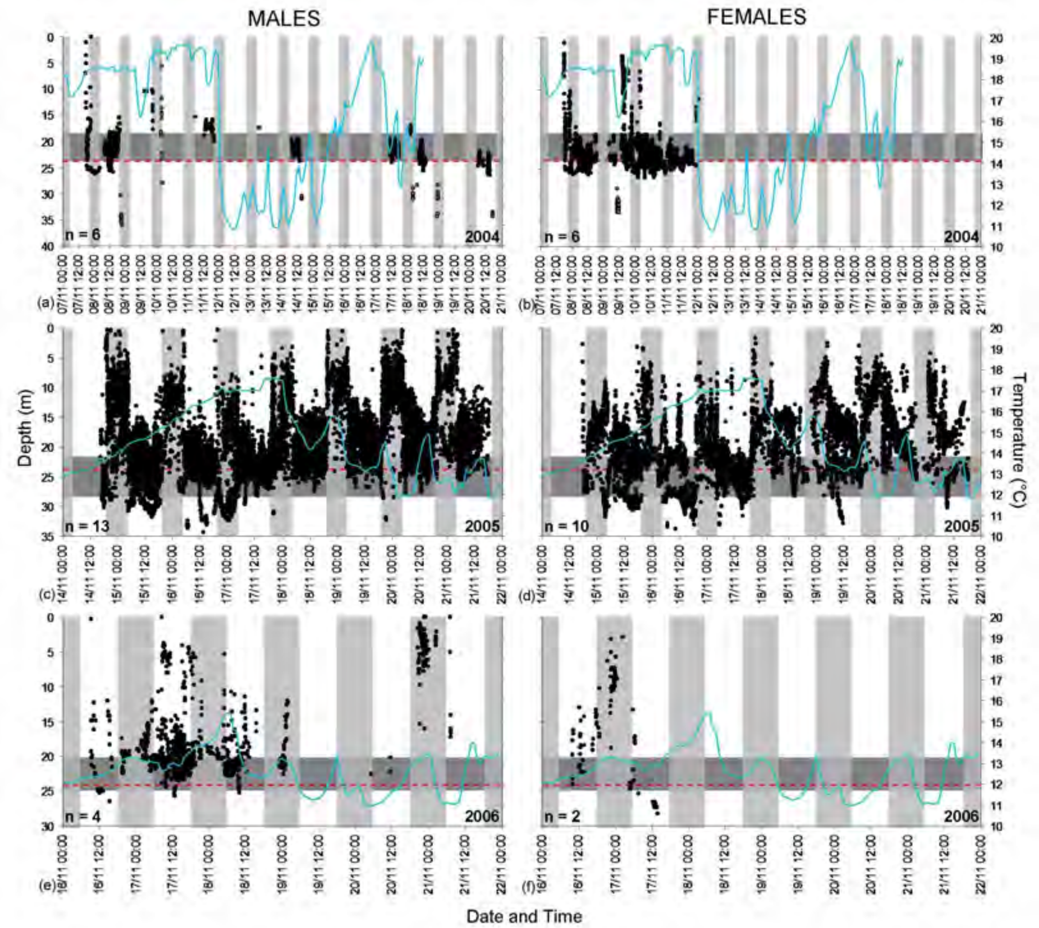


Figure 34: Depth plots of all male and female squid for the years (a and b) 2004, (c and d) 2005 and (e and f) 2006. Also shown is hourly bottom (24 m) temperature data (indicated by the red dotted line) measured at the squid buoy, day/night periods (night indicated by vertical shaded areas) and the bottom depth range of areas where VR2 receivers were deployed (indicated by horizontal shaded areas). Note: Due to the sloping of the sea floor as one moves offshore and the detection range of the VR2 receivers, it is possible for squid to be detected at a deeper depth than the depth range in which the VR2s were deployed.

Table XI: The results of two sample, two tailed t-tests to determine if significant differences (P<0.05) exist for (a) mean depth during the day versus night for male, female and all squid and (b) mean depth for males versus females during the day and night (b).

(a)	Category	Diurnal Period	n	mean depth (m) ± s.d.	tcalc	tcrit	P
2004	Males	Day	1 242	21.9 ± 2.2	-1.10	1.96	0.27
		Night	118	22.2 ± 6.9			
	Females	Day	2 297	22.2 ± 3.9	0.61	1.96	0.54
		Night	1 307	22.1 ± 2.6			
	All Squid	Day	3 539	22.1 ± 3.4	-0.31	1.96	0.75
		Night	1 425	22.1 ± 3.2			
2005	Males	Day	12 217	21.1 ± 4	67.61	1.96	0.00
		Night	5 678	15.5 ± 7.1			
	Females	Day	7 128	22.2 ± 4.9	37.09	1.96	0.00
		Night	2 899	17.9 ± 6.1			
	All Squid	Day	19 345	21.5 ± 4.4	76.28	1.96	0.00
		Night	8 577	16.3 ± 6.9			
2006	Males	Day	880	19.3 ± 4.3	14.19	1.96	0.00
		Night	351	14.6 ± 7.2			
	Females	Day	74	20.4 ± 4.9	8.39	1.98	0.00
		Night	38	11.3 ± 6.4			
	All Squid	Day	954	19.4 ± 4.3	16.05	1.96	0.00
		Night	389	14.3 ± 7.2			

(b)	Diurnal Period	Sex	n	mean depth (m) ± s.d.	tcalc	tcrit	P
2004	Day	Males	1 242	21.9 ± 2.2	-5.29	1.96	0.00
		Females	2 297	22.2 ± 3.9			
	Night	Males	118	22.2 ± 6.9	0.34	1.96	0.73
		Females	1 307	22.1 ± 2.6			
2005	Day	Males	12 217	21.1 ± 4.0	-16.42	1.96	0.00
		Females	7 128	22.2 ± 4.9			
	Night	Males	5 678	15.5 ± 7.1	-15.35	1.96	0.00
		Females	2 899	17.9 ± 6.1			
2006	Day	Males	880	19.3 ± 4.3	-2.02	1.96	0.04
		Females	74	20.4 ± 4.9			
	Night	Males	351	14.6 ± 7.2	2.73	1.97	0.01
		Females	38	11.3 ± 6.4			

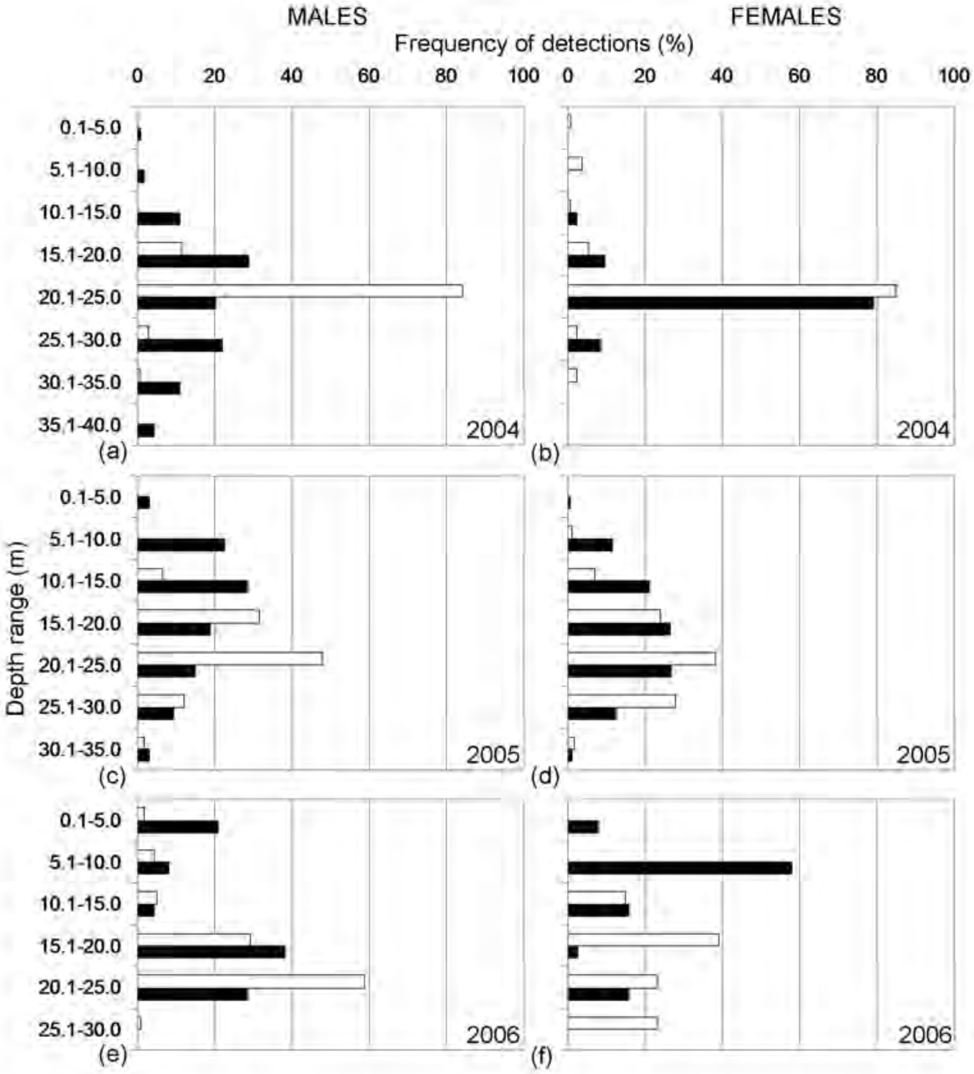


Figure 35: The frequency of detections recorded in different depth categories for males and females for the years (a and b) 2004, (c and d) 2005 and (e and f) 2006. White bars indicate the frequency of detections recorded during daylight hours whilst black bars indicate those recorded during the night.

5.3.4. Diurnal Behaviour

To identify diurnal patterns on the spawning sites, the percentage of transmissions successfully detected per hourly interval in a typical 24-hour period were plotted in Figure 36. This was done separately for males and females for each year, using the data from which duplicates had been removed.

A trend of a general increase in the percentage of detections recorded as dawn approaches and similarly a general decrease in detections after dusk exists for all years (Fig. 36a to d). This is most evident in the years 2003 (for males), 2004 (for males and females), 2005 (for males and females) and 2006 (for males). Interestingly, this general increase and decrease does not continue towards and beyond midday, respectively. Instead, peaks in the percentage of detections recorded throughout the day tended to vary between the years.

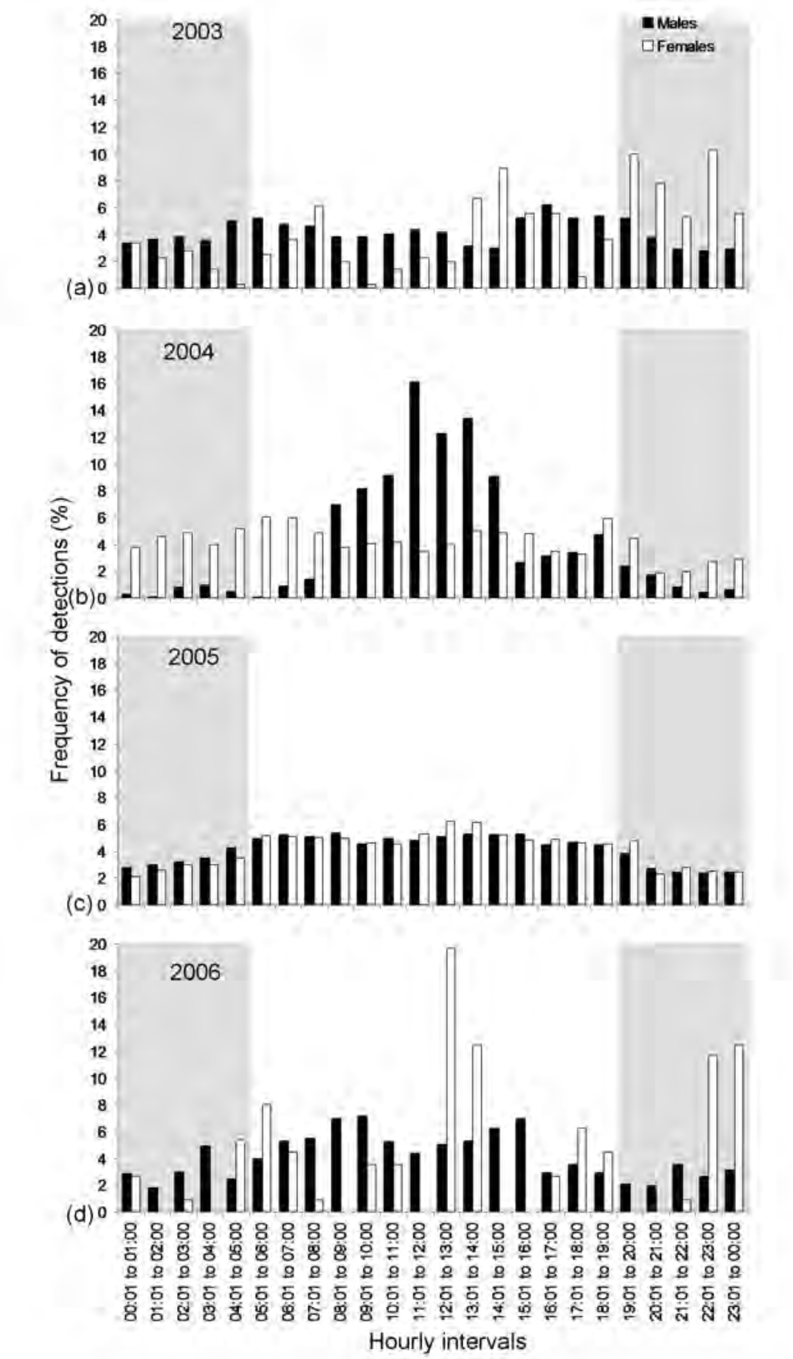


Figure 36: The frequency of detections recorded by the VR2 receivers during the hours of a typical day for the years (a) 2003 (n: males=5820, females=360), (b) 2004 (n: males=1360, females=3604), (c) 2005 (n: males=19 102, females=10 929) and (d) 2006 (n: males=1231, females=112). Periods of darkness are indicated by shaded areas and daylight by unshaded areas. (n refers to number of detections)

5.4. Discussion

5.4.1. "Presence-absence" behaviours

A previous acoustic telemetry study conducted in Oyster Bay (O'Dor *et al*. 1996; Sauer *et al*. 1997) showed that each dawn male squid moved onto the inshore spawning grounds, circling above egg beds, drawing in females and other males. Males and females formed pairs and mating and spawning activity commenced, often continuing for a number of hours after sunset. Females and sneaker males remained on the spawning site until their departure after dusk whereas males left the spawning site during the day, returning briefly before moving off at dusk. During this study, although monitoring was continuous, no acoustically tagged males or females were present on the spawning site between the hours of 18:00 and 04:00. Results from the current study however showed a mixed pattern of presence-absence on the spawning site, not solely related to day/night periods. Individuals of both sexes remained on the spawning site during some nights (Fig. 29-32). This was found for all years the study was conducted. No definite pattern of presence on the spawning site was found. However, three general "presence-absence behaviours" were identified. They can be described as (1) the arrival of individuals on the spawning site at dawn and departure at or shortly after dusk (2) the continuous and uninterrupted presence on the spawning site for a number of days and (3) presence on the spawning site interrupted by frequent yet short periods of absence. Certain individuals displayed only one type of presence-absence behaviour (Example F16, Fig. 31b) whereas others showed a combination of the three previously mentioned behaviours (Example M16, Fig. 31a). The presence-absence behaviours of individuals simultaneously present on the spawning site did not mirror one another. The driving force of these behaviours is therefore not related to environmental conditions. It is likely the overall condition of the animal, state of the gonads (ripe, partially spent or spent) and possibly reproductive success of an individual on a particular spawning site governs these movements. On average, males were found to spend more time on spawning sites than females (Table X). The variation in the amount of time individuals of both sexes spent on the spawning site however, varied greatly.

5.4.2. Movement between spawning sites

Previous studies on the inshore spawning grounds showed a great deal of emigration and immigration between spawning sites within an area (Lipinski 1994; Lipinski *et al.* 1998; Sauer *et al.* 1997; Sauer *et al.* 2000). The current study provides further evidence of this movement. In 2004 four individuals (M4, M6, M7 and F4) left the monitored spawning site and were shortly thereafter detected on a deeper spawning site off Cape St. Francis (Fig. 30b). On one occasion, M4 made the 1.7 km journey between these two sites at night. Movement between spawning sites is therefore not restricted to daylight hours.

5.4.3. Water column activity

After dusk the dense mating and spawning aggregations broke down, as has been observed in previous studies (Hanlon *et al.* 2002; Roberts 1998; Sauer *et al.* 1997; Sauer and Smale 1993). The majority of individuals remaining on the spawning sites moved higher up in the water column (Fig. 34). This distinct pattern in the vertical occupation of the water column is best illustrated in Figure 34c and d. Previous studies have shown squid caught on the spawning grounds at night have a higher percentage of food in their stomachs than squid caught during the day (Sauer and Lipinski 1991). Also the prey spectrum varies between day and night in that *Loligo reynaudii* dominates the diet of day caught squid (Sauer and Lipinski 1991). This indicates opportunistic feeding during the day. The diet of night caught squid includes benthic polychaetes and crustaceans as well as midwater prey (Sauer and Lipinski 1991). Sauer and Smale (1993) observed two principle forms of nocturnal feeding behaviour on the spawning grounds, namely feeding in the water column and what could possibly be benthic feeding. Individual squid disturbed the sand with their arms or with the water jet from their siphon. Another behaviour observed at night (Sauer *et al.* 1992; Sauer 1995b; Sauer and Smale 1993) is the deposition of egg strands by lone females, using stored spermatophores for fertilization. In the current study, detections recorded close to the bottom at night can probably be attributed to bottom feeding in male squid and a combination of bottom feeding and egg strand deposition in female squid.

The significantly shallower night-time depths for males and females (separately and combined) during the 2005 and 2006 experiments strongly indicates the primary nocturnal activity in these instances to be midwater feeding (Table XIa). This is reflected in Figure 35c to f where the frequency of occurrence in the shallower depth categories increases at night.

The mean depth of females during the day was significantly deeper than that for males in all three years pressure tags were used (Table XIb). A possible explanation lies in the sex ratio found on the inshore spawning grounds. The sex ratio (~2:1) is skewed towards males (Augustyn 1990; Hanlon *et al*. 2002; Sauer 1991) and males have to engage in agonistic bouts to gain access to females. It is therefore likely that tagged males were not paired and not participating in mating and spawning activity all of the time, resulting in the significantly shallower mean depth during the day. Females however (tagged individuals included) are likely to be paired and actively spawning when present on the spawning site. This is evident from diving observations during the day in which no lone females were seen in the water column or depositing egg strands (Sauer and Smale 1993). The significantly deeper mean depths of females during the day in the current study corresponds with these observations.

The comparison of mean depth of males and females at night provides some indication of the intensity of egg strand deposition by lone females. The significantly deeper night time depth for female squid in the 2005 study (Table XIb) suggests egg strand deposition by females was intense in the 2005 experiment. Figure 35 further illustrates the vertical occupation of tagged males and females during the day and night. Of interest is the distribution of both sexes throughout the water column at night, a result of the two different modes of feeding and continued spawning activity of females. Sauer (1995b) reported seeing squid in the top 5 m of the water column during two night dives, a phenomenon not observed during the day, as well as a few individuals throughout the water column.

5.4.4. Aggregation dynamics

It appears that on occasion a core aggregation of squid remains on the spawning site at night. Approaching dawn, more individuals arrive on the spawning site and the aggregation size increases, leading to an increase in the percentage of detections recorded during the day compared to during the night (Table IX). The early morning arrival of squid on the spawning site has been observed in a number of studies (O'Dor *et al*. 1996; Roberts 1998; Sauer *et al*. 1997) and is again indicated here by the general increase in the number of detections (Fig. 36). The peaks and troughs in the percentage of detections recorded in the hours between dawn and dusk (Fig. 36) are probably a result of immigration and emigration of tagged individuals to and from the monitored spawning sites. Figure 36 shows a general decrease in the number of detections after dusk as a result of large scale emigration from the spawning site. There is evidence to suggest those individuals leaving the spawning site after dusk either move offshore to feed (Sauer *et al*. 1997) or to other inshore spawning sites (this study).

It is a possible however that departures from inshore spawning sites are not entirely related to feeding. Several studies indicate a "resting" stage to occur in *L. reynaudii*. Evidence to support this theory includes the occasional presence of spent (Augustyn *et al*. 1994) and partially spent (Roberts 1998) squid on the inshore spawning grounds and individuals spawning several times during their lifecycle (Melo and Sauer 1999) with a peak in spring/early summer (Sauer *et al*. 1991). Serial spawning is a possible explanation for the long periods of absence from the inshore spawning sites (observed in this study) and movement between spawning sites over a number of weeks (Melo and Sauer 1999). Over time, spawning intensity decreases (Fig. 33).

5.4.5. Environmental effects on spawning aggregations

In the Roberts (1998) study, the formation of a spawning aggregation coincidently with an upwelling event led to the conclusion that upwelling may trigger spawning. The formation of a spawning aggregation shortly after upwelling in the 2006 acoustic telemetry study provides further evidence to support this theory (Fig. 28). Not only does upwelling enhance daily catches (Sauer 1991, Schön 2000), but it is possibly the most important environmental cue for spawning.

Upwelling events occurred during all four acoustic telemetry studies. The events occurring in 2004 and 2005 persisted for a number of days, and would have resulted in a drop in bottom temperature throughout Kromme Bay. Presence-absence (Fig. 30a) and depth data (Fig. 34a and b) recorded for individuals in 2004 suggest upwelling events with a rapid onset terminate spawning. Spawning activity was intense but ceased as bottom temperatures dropped and all the squid present left the spawning site. The decrease in VR2 receiver detection range (to 75 m) during thermocline conditions no doubt affected the number of detections recorded during upwelling events. However, the continual movement of squid around the spawning site, observed in this study (see Appendix A), ensured tagged individuals would move into this detection range on occasion. It is therefore unlikely a tagged individual went undetected when present on the spawning site. The sudden departure of squid from the spawning site as upwelling occurred in 2004, is therefore not a result of decreased detection range but rather a response to the sudden drop in temperature at the spawning site. This is possibly due to a physiological inability to acclimate quickly to the sudden drop in temperature rather than a response to the temperature itself, as *L. reynaudii* is known to spawn in deep water environments where bottom temperatures average ~10°C (Roberts *et al*. 2002).

Similar to the 2004 upwelling event, the event occurring during the 2003 study also had a rapid onset and bottom temperatures dropped suddenly. Squid behaviour in the 2003 study however, contrasts with that seen at the onset of the 2004 upwelling event. The two males present on the spawning site as upwelling occurred both remained on the site during the event (Fig. 29a). Due to the lack of pressure data however, it cannot be said for certain whether these males were engaged in spawning activity or moved higher up in the water column and remained above the thermocline. As upwelling occurred in 2004, one individual was seen to move up in the water column (Fig. 34b), above the thermocline, before leaving the spawning site. The movement of the two male squid to a position above the thermocline is therefore certainly a possibility but the fact that they could have been engaged in spawning activity cannot be ignored.

From the findings of Chapter 4 however, it is unlikely that a short duration upwelling event, such as the 2003 event (Fig. 29a) recorded at the thermistor array site, resulted in a drop in bottom temperature at the 2003 monitored spawning site. This spawning site was located at site 1, where the additional UTR was deployed for the temperature comparison study in Chapter 4. The combined effect of the time lag in the drop of temperatures between the thermistor array site (site 2) and the spawning site (site 1), and the stronger post-upwelling westerly wind causing downwelling possibly resulted in a reversal of upwelling before the cold water could move further into the bay (Fig. 29b). This could explain the presence of the two male squid on the spawning site during the sudden drop in bottom temperature recorded at the thermistor array site. It is likely this drop in bottom temperature did not occur on the spawning site.

Spawning behaviour throughout the 2005 experiment (Fig. 31a and b, Fig. 33 c and Fig. 34c and d) was intense, even during the upwelling event. This event had a gradual onset and spawning continued uninterrupted. It appears sudden and extreme changes in temperature, resulting from rapid onset major upwelling events, disrupt spawning. However, previous studies have shown a positive relationship to exist between squid catches and upwelling (Roberts and Sauer 1994; Sauer *et al*. 1991; Schön 2000). Results from the current study suggest squid spawn in a temperature range of 11.5-19.5 °C. It is possible squid do prefer bottom temperatures in the lower part of this temperature range (i.e. 11.5 °C to 16 °C) which would result from minor upwelling events and explain the positive relationship between upwelling and catches. The upwelling events would have to have a gradual onset in order not to disrupt spawning however.

The small boat CTD survey (Chapter 4) showed considerable spatial variability to exist in turbidity levels within Kromme Bay. Therefore, the only accurate and relevant turbidity data would be that recorded in 2005, by the OBS-3A deployed on the monitored spawning site, in the centre of the VR2 array. Although no major turbidity events were recorded at the thermistor array site in 2004, this does not indicate low turbidity levels elsewhere in Kromme Bay and hence on the monitored spawning site. Similarly the major turbidity event recorded at the thermistor array site in 2003 does not indicate a turbidity event to have occurred at the spawning site. Indeed, video footage from the spawning site, recorded during the 4.5 day turbidity event at the thermistor array site, show good visibility (3-5 m) which would equate to <10 NTU's (Dorfler 2002). It can be surmised that turbidity levels remained low at the spawning site in 2003. As the only accurate and relevant turbidity data was recorded in 2005 and turbidity levels remained <8 NTU's, no conclusions regarding the effect of high turbidity can be drawn from the current study. Dorfler (2002) however, showed an increase in turbidity resulted in a rapid decline in squid catches. As discussed previously, visual communication is essential to pair formation, mating and the spawning process. Increased turbidity resulting in decreased visibility would disrupt visual communication, hence disrupting spawning.

5.5. Conclusions

Three general presence-absence behaviours are found on spawning sites. They can be described as (1) arrival at dawn and departure after dusk, (2) a continuous and uninterrupted presence for a number of days and (3) presence interrupted by frequent but short periods of absence. Despite these different behaviours, on occasion a core aggregation of squid remains on "active" spawning sites at night. The formation of such aggregations is likely triggered by upwelling events. As dawn approaches, more individuals arrive on the spawning site and the aggregation size increases (Fig. 37a). During the day, the aggregation is dense, made up of mating pairs (Fig. 37c), pairs depositing egg strands (Fig. 37d), lone consort males (Fig. 37e), males engaged in agonistic behaviour (Fig. 37f) and lone sneaker males (Fig. 37g). Partially spent and spent individuals move offshore for a "resting" period whilst ripe individuals move between spawning sites (Fig. 37b). Shortly after dusk, pair formation breaks down and some individuals leave the spawning site, moving offshore to feed or rest (Fig. 37h). It is thought head-to-head mating occurs offshore (Fig. 37m). Those individuals remaining on the spawning site at night search for prey throughout the water column (Fig. 37k) and in the benthos (Fig. 37l) whilst lone females deposit egg strands (Fig. 37j). Movement between the spawning sites continues at night (Fig. 37i). This study has also shown rapid changes in temperature, such as sudden upwelling events, to possibly disrupt spawning activity for a short time. Further investigation is needed to confirm this. Gradual temperature changes however, do not disrupt spawning activity.

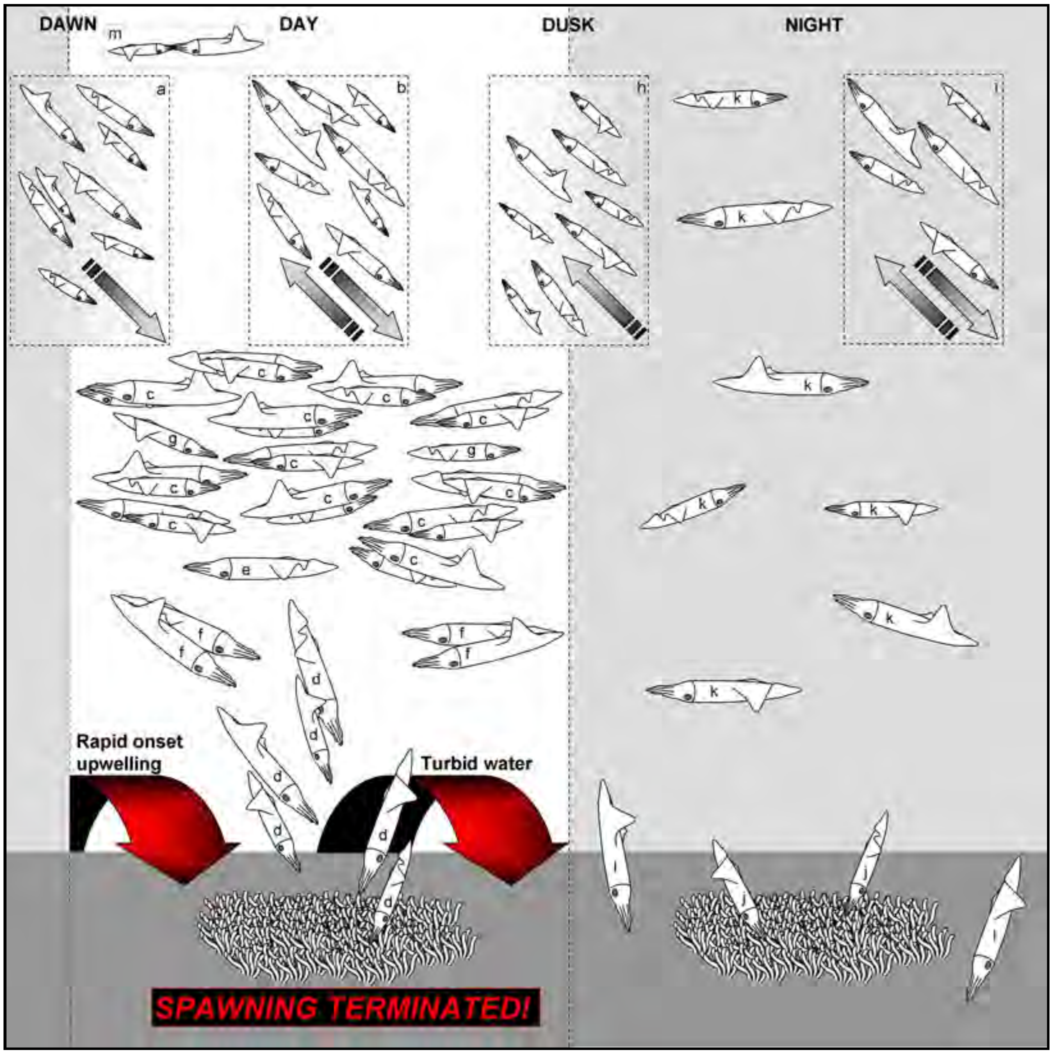


Figure 37: Schematic representation of activities on the spawning sites during the day and at night. At dawn (a) a large number of individuals arrive on the spawning site and the aggregation size increases. (b) Throughout the day partially spent and spent individuals move offshore for a "resting" period while ripe individuals move to and from spawning sites. (c) During the day a dense concentration of paired males and females, (d) female squid, accompanied by males, depositing egg strands, (e) lone consort males, (f) male squid engaged in agonistic bouts and (g) sneaker males forms. After dusk, (h) this dense aggregation breaks down and a number of squid move offshore. (i) A loose aggregation of squid remains on the spawning site and movement between spawning sites continues. (j) Lone females continue to deposit egg strands while (k) other individuals search for food in the water column and (l) the benthos. It is thought (m) head-to-head mating and the deposition of spermatophores into the females' buccal mass occurs offshore. The process of pair formation, mating and spawning is possibly triggered by upwelling events (resulting in cooler bottom temperatures) and briefly disrupted (due to physiological inability to quickly adapt to cold temperatures), once initiated, by rapid onset upwelling.

CHAPTER 6

Summary of Conclusions and recommendations for future research

The main aims of this research were: (1) to determine the immediate response of spawning squid to environmental changes, specifically upwelling and turbidity events and (2) to add to existing knowledge of spawning behaviour and movement on spawning grounds. The approach taken in this study was to use acoustic telemetry equipment to monitor individual squid within spawning aggregations whilst simultaneously monitoring temperature and turbidity conditions within Kromme Bay. It was later deemed necessary to investigate the integrity of the telemetry system used and the spatial variation of environmental conditions within the bay. This was to allow for the accurate interpretation of acoustic telemetry data.

The main findings were:

The integrity of the telemetry system

- The hexagonal VR2 receiver array design used resulted in a detection range of 75 m and "acoustic dead zones" as wide as 350 m between receivers during thermocline conditions.
- However, in isothermic conditions "acoustic dead zones" are absent and a total area of 1.28 km^2 can be monitored.
- The placement of VR2 receivers is a trade-off between monitoring as large an area as possible without increasing the extent of "acoustic dead zones" resulting from various environmental conditions.
- The hexagonal configuration of VR2 receivers is well suited to monitor the movement of squid on spawning sites.
- The system used in this study can support a maximum of seven tagged squid and two tagged predators at one time.

Spatial variation in environmental conditions within Kromme Bay

- Temperatures recorded at the thermistor array site were similar to those experienced throughout the bay.
- Upwelling events of long duration perpetuated throughout the bay. i.e.: an upwelling event at the thermistor array site would eventually be experienced at spawning sites within Kromme Bay.
- Upwelling events of short duration, resulting from strong post-upwelling westerly winds causing sudden downwelling and hence an immediate increase in bottom temperature, did not perpetuate throughout the bay. i.e. an event such as this occurring at the thermistor array site would not perpetuate throughout the bay and no sudden drop in bottom temperature would occur at other sites in the bay.
- A great deal of spatial variability exits regarding turbidity levels within Kromme Bay.
- Turbidity levels recorded at the thermistor array site were a poor indication of turbidity levels elsewhere in the bay.

Spawning behaviour and movement on spawning sites

- Three general "presence-absence" behaviours are found on spawning sites.
  (1) arrival at dawn and departure after dusk
  (2) a continuous and uninterrupted presence for a number of days
  (3) presence interrupted by frequent but short periods of absence.
- It appears on occasion a core aggregation of squid remains on "active" spawning sites at night.
- As dawn approaches, more individuals arrive on the spawning site and the aggregation size increases.
- During the day, the aggregation is dense, made up of mating pairs, pairs depositing egg strands, lone consort males, males engaged in agonistic behaviour and lone sneaker males.

- Partially spent and spent individuals move offshore for a "resting" period whilst ripe individuals move between spawning sites. Shortly after dusk, pair formation breaks down and some individuals leave the spawning site, moving offshore to feed or rest.
- Those individuals remaining on the spawning site search for prey throughout the water column and in the benthos whilst lone females deposit egg strands.
- Movement between spawning sites continues at night.

The response of spawners to environmental changes

- This study finds further evidence to support the hypothesis that upwelling triggers spawning.
- Spawning activity is possibly disrupted and individuals leave the spawning site in response to rapid onset, major upwelling events.
- Spawning activity continues uninterrupted during upwelling events with a gradual onset.
- No conclusions regarding responses to increased turbidity levels can be drawn from the current study, however, high turbidity levels would disrupt spawning due to reduced visibility.

Recommendations for future research:

The thermistor array in Kromme Bay has been used as an environmental monitoring mooring for many projects in the past. A number of instruments measuring temperature, turbidity, currents and wave height have been deployed on this mooring and the data used in large scale, long-term research projects. A study such as the one reported on in this thesis, which examines the immediate response of animals to environmental conditions over a short time period however, requires more fine scale data. The current research project has shown there to be a certain degree of temperature variability within Kromme Bay, although long duration upwelling and downwelling events do perpetuate throughout the bay. In terms of turbidity levels, this spatial variation can at times be very great. For this reason, future acoustic telemetry experiments should incorporate environmental monitoring instruments into the VR2 receiver array. In addition, data recorded by the passive tracking acoustic telemetry system described in this work, could be supplemented by active tracking of individual squid during the day and at night.

REFERENCES

ACOLAS,M.L., BÉGOUT ANRAS,M.L., VÉRON,V., JOURDAN,H., SABATIÉ,M.R. and BAGLINIÈRE,J.L. 2004. An assessment of the upstream migration and reproductive behaviour of allis shad (*Alosa alosa* L.) using acoustic tracking. *ICES Journal of Marine Science 61: 1291-1304.*

ACOLAS,M.L., VÉRON,V., JOURDAN,H., BÉGOUT,M.L., SABATIÉ,M.R. and BAGLINIÈRE,J.L. 2006. Upstream migration and reproductive patterns of a population of allis shad in a small river (L'Aulne, Brittany, France). *ICES Journal of Marine Science 63: 476-484.*

AITKEN,J.P., O'DOR,R.K. and JACKSON,G.D. 2005. The secret life of the giant Australian cuttlefish *Sepia apama* (Cephalopoda): Behaviour and energetics in nature revealed through radio acoustic positioning and telemetry (RAPT). *Journal of Experimental Marine Biology and Ecology 320: 77-91.*

ALMEIDA,P.R. 1996. Estuarine movement patterns of adult thin-lipped grey mullet, *Liza ramada* (Risso) (Pisces, Mugilidae), observed by ultrasonic tracking. *Journal of Experimental Marine Biology and Ecology 202: 137-150.*

AUGUSTYN,C.J. 1990. Biological studies on the chokker squid *Loligo vulgaris reynaudii* (Cephalopoda; Myopsida) on spawning grounds off the south-east coast of South Africa. *South African Journal of Marine Science 9: 11-26.*

AUGUSTYN,C.J. 1989. Systematics, life cycle and resource potential of the chokker squid *Loligo vulgaris reynaudii*. Unpublished Ph.D. Thesis. University of Port Elizabeth. *378 pp*.

AUGUSTYN,C.J. 1991. The biomass and ecology of chokka squid *Loligo vulgaris reynaudii* off the west coast of South Africa. *South African Journal of Zoology 26(4): 164-181.*

AUGUSTYN,C.J. 1986. The squid jigging fishery on the South African south coast. *South African Shipping News and Fishing Industry Review 41(5): 24-26.*

AUGUSTYN,C.J., LIPINSKI,M.R., SAUER,W.H.H., ROBERTS,M.J. and MITCHELL-INNES,B.A. 1994. Chokka squid on the Agulhas Bank: life history and ecology. *South African Journal of Science 90: 143-154.*

AUGUSTYN,C.J. and ROEL,B.A. 1998. Fisheries biology, stock assessment, and management of the chokka squid (*Loligo vulgaris reynaudii*) in South African water: an overview. *California Cooperative Oceanic Fisheries Investigations Reports 39: 71-80.*

BAKUN,A. and CSIRKE,J. 1998. Environmental processes and recruitment variability. In *Squid Recruitment Dynamics. The Genus Illex as a Model. The Commercial Illex Species. Influences on Variability*. (ed.) Rodhouse,P., Dawe,E.G. & O'Dor,R.K. Vol. 376 edn. Vol FAO Fisheries Technology Paper, *273-*

BECKLEY,L.E. 1983. Sea-surface temperature variability around Cape Recife, South Africa. *South Africa Journal of Science 79: 436-438.*

BIRCH,G.F. 1981. Bathymetry and geomorphology of the Cape Seal to Cape Recife inner shelf. *Transactions, Geological Society of South Africa 84: 233-237.*

BRILL,R.W., BALAZS,G.H., HOLLAND,K.N., CHANG,R.K.C., SULLIVAN,S. and GEORGE,J.C. 1995. Daily movements, habitat use, and submergence intervals of normal and tumor-bearing juvenile green turtles (*Chelonia mydas* L.) within a foraging area in the Hawaiian islands. *Journal of Experimental Marine Biology and Ecology 185: 203-218.*

BROOKING,P., DOUCETTE,G., TINKER,S. and WHORISKEY,F.G. 2006. Sonic tracking of wild cod, *Gadus morhua*, in an inshore region of the Bay of Fundy: a contribution to understanding the impact of cod farming for wild cod and endangered salmon populations. *ICES Journal of Marine Science 63(7): 1364-1371.*

CARR,J.W., LACROIX,G.L., ANDERSONS,J.M. and DILWORTH,T. 1997. Short communication: Movements of non-maturing cultured Atlantic salmon (*Salmo salar*) in a Canadian River. *ICES Journal of Marine Science 54: 1082-1085.*

CARR,S.D., TANKERSLEY,R.A., HENCH,J.L., FORWARD,R.B. and LUETTICH,R.A. 2004. Movement patterns and trajectories of ovigerous blue crabs *Callinectes sapidus* during spawning migration. *Estuarine, Coastal and Shelf Science 60: 567-579.*

COCHRANE,K.L., BUTTERWORTH,D.S. and PAYNE,A.I.L. 1997. South Africa's offshore living marine resources: the scientific basis for management of the fisheries. *Transactions of the Royal Society of South Africa 52: 149-176.*

COOKE,S.J. and PHILIPP,D.P. 2004. Behaviour and mortality of caught-and-released bonefish (*Albula* spp.) in Bahamian waters with implications for a sustainable recreational fishery. *Biological Conservation 118: 599-607.*

CUCCU,D., JEREB,P., RAGONESE,S., GIOVANNINI,N., COLELLA,S. and CAU,A. 2008. On the abundance and spatial distribution of *Illex coindetii* and *Eledone moschata* in the Sardinian Seas (central-western Mediterranean)-A preliminary and qualitative investigation with special attention to some environmental constraints. *Bollettino Malacologico 54: 15-25.*

DE WET,W. 1995. Gonad histology, fecundity and fecundity and reproductive behaviour of the chokka squid, *Loligo vulgaris reynaudii*. Unpublished M.Sc. Dissertation. University of Port Elizabeth. *97 pp*.

DORFLER,K. 2002. The dynamics of turbidity on the spawning grounds of the chokka squid *Loligo vulgaris reynaudii* and links to squid catches. Unpublished M.Sc. Dissertation. University of Port Elizabeth. *157 pp*.

EGLI,D.P. and BABCOCK,R.C. 2004. Ultrasonic tracking reveals multiple behavioural modes of snapper (*Pagrus auratus*) in a temperate no-take marine reserve. *ICES Journal of Marine Science 61: 1137-1143.*

GIRARD,C., BENHAMOU,S. and DAGORN,L. 2004. FAD: Fish Aggregating Device or Fish Attracting Device? A new analysis of yellowfin tuna movements around floating objects. *Animal Behaviour 67: 319-326.*

GOSCHEN,W.S. and SCHUMANN,E.H. 1995. Upwelling and the occurance of cold water around Cape Recife, Algoa Bay, South Africa. *South African Journal of Marine Science 16: 57-67.*

HANLON,R.T. 1998. Mating systems and sexual selection in the squid *Loligo*: How might commercial fishing on spawning squids affect them? *California Cooperative Oceanic Fisheries Investigations Reports 39: 92-100.*

HANLON,R.T., MAXWELL,M.R. and SHASHAR,N. 1997. Behavioural dynamics that would lead to multiple paternity within egg capsules of the squid *Loligo pealeii*. *Biology Bulletin 193: 212-214.*

HANLON,R.T., SMALE,M.J. and SAUER,W.H.H. 1994. An ethogram of body patterning behaviour in the squid *Loligo vulgaris reynaudii* on spawning grounds in South Africa. *Biology Bulletin 187: 363-372.*

HANLON,R.T., SMALE,M.J. and SAUER,W.H.H. 2002. The mating system of the squid *Loligo vulgaris reynaudii* (Cephalopoda, Mollusca) off South Africa: Fighting, guarding, sneaking, mating and egg laying behaviour. *Bulletin of Marine Science 71(1): 331-345.*

HASTIE,L.C., JOY,J.B., PIERCE,G.J. and YAU,C. 1994. Reproductive biology of *Todaropsis eblanae* (Cephalopoda: Ommastrephidae) in Scottish waters. *Journal of the MarineBiological Association of the United Kingdom 74: 367-382.*

HEUPEL,M.R., SEMMENS,J.M. and HOBDAY,A.J. 2006. Automated acoustic tracking of aquatic animals: scales, design and deployment of listening station arrays. *Marine and Freshwater Research 57: 1-13.*

HEUPEL,M.R., SIMPFENDORFER,C. and LOWE,C. 2005. Passive Acoustic Telemetry Technology: Current Applications and Future Directions. Mote Technical Report (1066). *http://www. vemco. com*

HOGAN,Z. 2003. New methods for the study of fish migrations in large rivers: Examples from the Mekong River Basin . Unpublished.

HUMSTON,R.J., AULT,J.S., LARKIN,M.F. and LUO,J. 2005. Movements and site fidelity of the bonefish *Albula vulpes* in the northern Florida Keys determined by acoustic telemetry. *Marine Ecology Progress Series 291: 237-248.*

JADOT,C., DONNAY,A., ACOLAS,M.L., CORNET,Y. and BÉGOUT ANRAS,M.L. 2006. Activity patterns, home-range size, and habitat utilization of *Sarpa sarpa* (Teleostei: Sparidae) in the Mediterranean Sea. *ICES Journal of Marine Science 63: 128-139.*

JEREB,P., CUCCU,D., GIORDANO,G., MAIORANO,P. and RAGONESE,S. 2005. Using historical series of trawl surveys data to investigate cephalopods: a new method of exploratory analysis. *Biologia Marina Mediterranea 12: 526-530.*

JEREB,P., MASSI,D., NORRITO,G. and FIORENTINO,F. 2001. Preliminary observations of environmental effects on spatial distribution and abundance of *Eledone cirrhosa* and *Illex coindetii* in the Strait of Sicily (Central Mediterranean Sea). *ICES CM 2001/K: 34-*

JOSUPEIT,H. 2005. Squid market report-December 2005. *http://www. globefish. org*

LEFKADITOU,E., SANCHEZ,P., TSANGRIDIS,A. and ADAMIDOU,A. 1998. A preliminary investigation on how meteorological changes may affect beach-seine catches of *Loligo vulgaris* in the Thracian Sea (Eastern Mediterranean). *South African Journal of Marine Science 20: 453-461.*

LIPINSKI,M.R. 1994. Differences among basic biological parameters in a population of chokka squid *Loligo vulgaris reynaudii* (Cephalopda: Loliginidae) sampled by three methods. *South African Journal of Marine Science 24: 281-286.*

LIPINSKI,M.R., HAMPTON,I., SAUER,W.H.H. and AUGUSTYN,C.J. 1998. Daily net emigration from a spawning concentration of chokka squid (*Loligo vulgaris reynaudii* d'Orbigny, 1845) in Kromme Bay South Africa. *ICES Journal of Marine Science 55: 258-270.*

LLORET,J., LLEONART,J., SOLE,I. and FROMENTIN,J.M. 2001. Fluctuations of landings and environmental conditions in the North-Western Mediterranean Sea. *Fisheries Oceanography 10: 33-50.*

LØKKEBORG,S., SKAJAA,K. and FERNÖ,A. 2000. Food-search strategy in ling (*Molva molva* L.): Crepuscular activity and use of space. *ICES Journal of Marine Science 247: 195-208.*

MELO,Y.C. and SAUER,W.H.H. 1999. Confirmation of serial spawning in the chokka squid *Loligo vulgaris reynaudii* off the coast of South Africa. *Marine Biology 135: 307-313.*

MITAMURA,H., ARAI,N., SAKAMOTO,W., MITSUNAGA,Y., TANAKA,H., MUKAI,Y., NAKAMURA,K., SASAKI,M. and YONEDA,Y. 2005. Role of olfaction and vision in homing behaviour of black rockfish *Sebastes inermes*. *Journal of Experimental Marine Biology and Ecology 322: 123-134.*

MORENO,A.F., AZEVEDO,M., PEREIRA,J. and PIERCE,G.J. 2007. Growth strategies in the squid *Loligo vulgaris* from Portuguese waters. *Marine Biology Research 3: 49-59.*

O'DOR,R.K., WEBBER,D.M., SAUER,W.H.H., ROBERTS,M.J. and SMALE,M.J. 1996. High resolution, 3-D tracking of squid on spawning grounds. In *Proceedings of the 13th International Symposium on Biotelemetry, Williamsburg, Virginia, March 1995*. (ed.) Cristalli,C., Amlaner,C.J. & Neuman,M.R.Fayetteville, University of Arkansas Press:*193-198*.

PIERCE,G.J., BAILEY,N., STRATOUDAKIS,Y. and NEWTON,A. 1998. Distribution and abundance of the fished population of *Loligo forbesi* in Scottish waters: analysis of research cruise data. *ICES Journal of Marine Science 55: 14-33.*

PIERCE,G.J., VALAVANIS,V.D., GUERRA,A., JEREB,P., ORSI-RELINI,L., BELLIDO,J.M., KATARA,I., PIATKOWSKI,U., PEREIRA,J., BALGUERIAS,E., SOBRINO,I., LEFKADITOU,E., WANG,J., SANTURTUN,M., BOYLE,P.R., HASTIE,L.C., MACLEOD,C.D., SMITH,J.M., VIANA,M., GONZÁLEZ,A.F. and ZUUR,A.F. 2008. A review of cephalopod-environment interactions in European Seas. *Hydrobiologia 612: 49-70.*

PINCOCK,D.G. and VOEGELI,F.A. 2002. Quick course in underwater telemetry systems. Unpublished.

RASERO,M. 1994. Relationship between cephalopod abundance and upwelling: the case of *Todaropsis eblanae* (Cephalopoda: Ommastrephidae) in Galician waters (NW Spain). *ICES CM 1994/K: 40-*

RIGBY,P.R. 2000. Does tagging for radio acoustic positioning telemetry change spawning behaviour of chokka squid, *Loligo vulgaris reynaudii*? Unpublished M.Sc. Dissertation. Dalhousie University. *149 pp*.

ROBERTS,M.J. 1998. The influence of the environment on chokka squid *Loligo vulgaris reynaudii* spawning aggregations: Steps towards a quantified model. *South African Journal of Marine Science 20: 267-284.*

ROBERTS,M.J., BARANGE,M., LIPINSKI,M.R. and PROWSE,M.R. 2002. Direct hydroacoustic observations of chokka squid *Loligo vulgaris reynaudii* spawning activity in deep water. *S. Afr. J. mar. Sci 24: 387-393.*

ROBERTS,M.J. and SAUER,W.H.H. 1994. Environment: the key to understanding the South African chokka squid (*Loligo vulgaris reynaudii*) life cycle and fishery? *Antarctic Science 6(2): 249-258.*

ROBERTS,M.J. and VAN DEN BERG,M. 2002. Recruitment variability of chokka squid (*Loligo vulgaris reynaudii*) - Role of currents on the Agulhas Bank (South Africa) in paralarvae distribution and food abundance. *Bulletin of Marine Science 71(2): 691-710.*

ROBICHAUD,D. and ROSE,G.A. 2003. Sex differences in cod residency on a spawning ground. *Fisheries Research 60: 33-43.*

SACAU,M., PIERCE,G.J., WANG,J., ARKHIPKIN,A.I., PORTELA,J., BRICKLE,P., SANTOS,M.B. and CARDOSA,X. 2005. The spatiotemporal pattern of Argentine shortfin squid *Illex argentinus* abundance in the southwest Atlantic. *Aquatic Living Resources 18: 361-372.*

SAUER,W.H.H. 1991. Population characteristics of the chokker squid, *Loligo vulgaris reynaudii*, and its distribution in the Algoa Bay-St Francis Bay area in relation to environmental conditions. Unpublished M.Sc. Dissertation. University of Port Elizabeth. *87 pp*.

SAUER,W.H.H. 1995a. South Africa's Tsitsikamma National Park as a protected breeding area for the commercially exploited chokka squid *Loligo vulgaris reynaudii*. *South African Journal of Marine Science 16: 365-371.*

SAUER,W.H.H. 1995b. The impact of fishing on chokka squid *Loligo vulgaris reynaudii* concentrations on inshore spawning grounds in the South-Eastern Cape, South Africa. *South African Journal of Marine Science 16: 185-193.*

SAUER,W.H.H., GOSCHEN,W.S. and KOORTS,A.S. 1991. A preliminary investigation of the effect of sea temperature fluctuations and wind direction on catches of chokka squid *Loligo vulgaris reynaudii* off the Eastern Cape, South Africa. *South African Journal of Marine Science 11: 467-473.*

SAUER,W.H.H. and LIPINSKI,M.R. 1991. Food of squid *Loligo vulgaris reynaudii* (Cephalopoda: Loliginidae) on their spawning grounds off the Eastern Cape, South Africa. *South African Journal of Marine Science 10: 193-201.*

SAUER,W.H.H., LIPINSKI,M.R. and AUGUSTYN,C.J. 2000. Tag recapture studies of the chokka squid *Loligo vulgaris reynaudii* d'Orbigny, 1845 on inshore spawning grounds on the south-east coast of South Africa. *Fisheries Research 45: 283-289.*

SAUER,W.H.H., MCCARTHY,C., SMALE,M.J. and KOORTS,A.S. 1993. An investigation of the egg distribution of the chokka squid, *Loligo vulgaris reynaudii*, in Krom Bay, South Africa. *Bulletin of Marine Science 53(3): 1066-1077.*

SAUER,W.H.H., ROBERTS,M.J., LIPINSKI,M.R., SMALE,M.J., HANLON,R.T., WEBBER,D.M. and O'DOR,R.K. 1997. Choreography of the squid's "nuptial dance". *Biology Bulletin 192: 203-207.*

SAUER,W.H.H. and SMALE,M.J. 1993. Spawning behaviour of *Loligo vulgaris reynaudii* in shallow coastal waters of the south-Eastern Cape, South Africa. In *Recent Advances in Fisheries Biology*. (ed.) Okutani,T., O'Dor,R.K. & Kubodera,T.Tokyo, Tokai University Press:*489-498*.

SAUER,W.H.H., SMALE,M.J. and LIPINSKI,M.R. 1992. The location of spawning grounds, spawning and schooling behaviour of the squid *Loligo vulgaris reynaudii* (Cephalopoda: Myopsida) off the Eastern Cape coast, South Africa. *Marine Biology 114: 97-107.*

SCHÖN,P. 2000. An investigation into the influence of the environment on spawning aggregations and jig catches of chokka squid *Loligo vulgaris reynaudii* off the coast of South Africa. Unpublished Ph.D. Thesis. University of Port Elizabeth. *130 pp*.

SCHUMANN,E.H. 1999. WInd-driven mixed layer and coastal upwelling processes off the south coast of South Africa. *Journal of Marine Research 57: 671-691.*

SCHUMANN,E.H., CHURCHILL,J.R.S. and ZAAYMAN,H.J. 2005. Oceanic variability in the western sector of Algoa Bay, South Africa. *African Journal of Marine Science 27(1): 65-80.*

SCHUMANN,E.H., PERRINS,L. and HUNTER,I.T. 1982. Upwelling along the south coast of the Cape Province, South Africa. *South African Journal of Science 78: 238-242.*

SCHUMANN,E.H., ROSS,G.J.B. and GOSCHEN,W.S. 1988. Cold water events in Algoa Bay and along the Cape south coast, South Africa, in March / April 1987. *South African Journal of Marine Science 84: 579-584.*

SIMPFENDORFER,C., HEUPEL,M.R. and HUETER,R.E. 2002. Estimation of short-term centers of activity from an array of omnidirectional hydrophones and its use in studying animal movements. *Canadian Journal of Fisheries and Aquatic Science 59: 23-32.*

SMALE,M.J., SAUER,W.H.H. and ROBERTS,M.J. 2001. Behavioural interactions of predators and spawning chokka squid off South Africa: towards quantification. *Marine Biology 139: 1095-1105.*

VABØ,R., HUSE,G., FERNÖ,A., JØRGENSEN,T., LØKKEBORG,S. and SKARET,G. 2004. Simulating search behaviour of fish towards bait. *ICES Journal of Marine Science 61: 1224-1232.*

VALAVANIS,V.D., GEORGAKARAKOS,S., KAPANTAGAKIS,A., PALIALEXIS,A. and KATARA,I. 2004. A GIS environmental modelling approach to essential fish habitat designation. *Ecological Modelling 178: 417-427.*

VALAVANIS,V.D., KATARA,I. and PALIALEXIS,A. 2005. Marine GIS: identification of mesoscale oceanic thermal fronts. *InternationalJournal of Geographical Information Science 19: 1131-1147.*

WALUDA,C.M., GRIFFITHS,H.J. and RODHOUSE,P. 2008. Remotely sensed spatial dynamics of the *Illex argentinus* fishery Southwest Atlantic. *Fisheries Research 91: 196-202.*

WALUDA,C.M. and PIERCE,G.J. 1998. Temporal and spatial patterns in the distribution of squid *Loligo* spp. in United Kingdom waters. *S. Afr. J. mar. Sci 20: 323-336.*

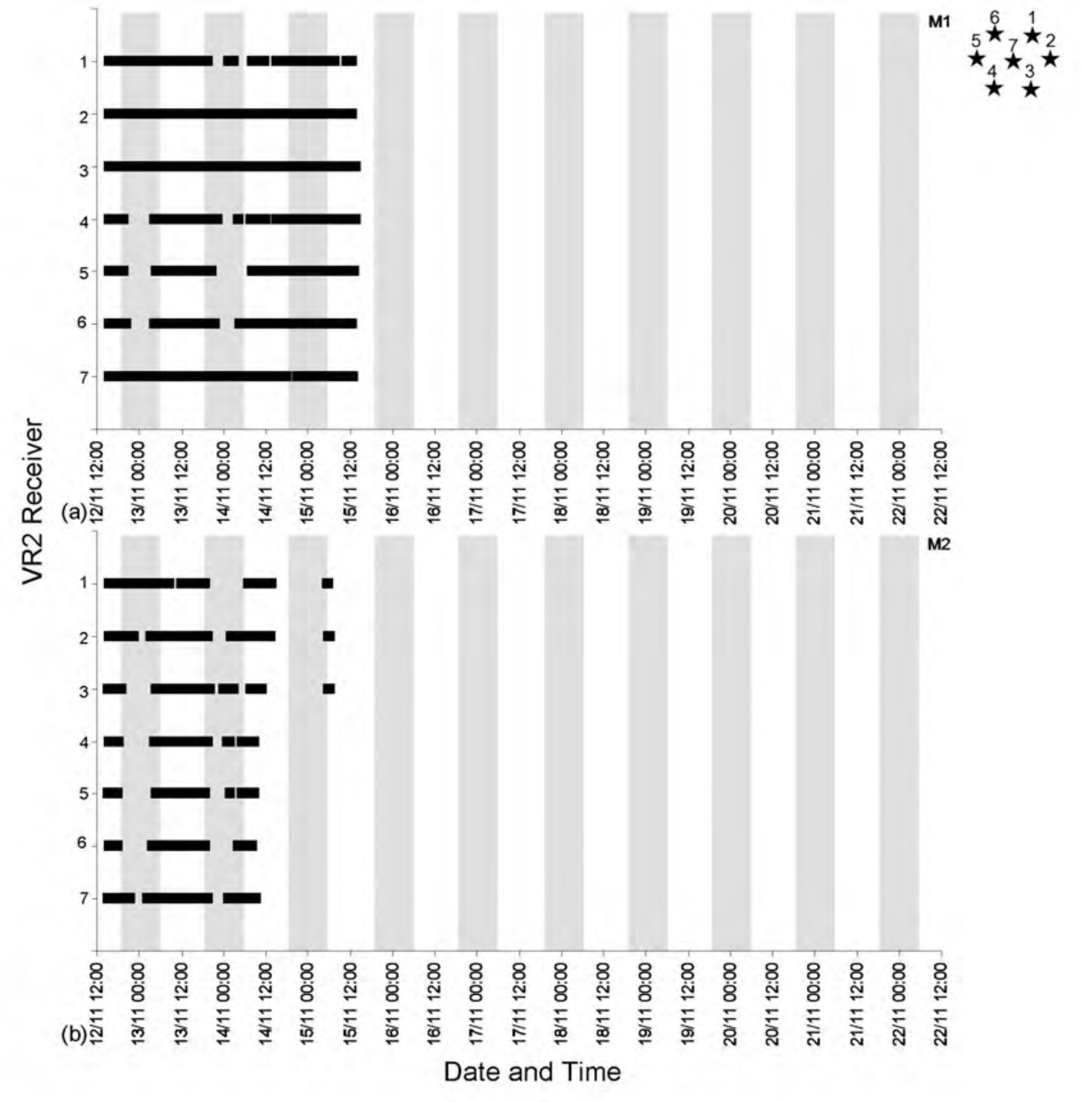
WALUDA,C.M., RODHOUSE,P., TRATHAN,P.N. and PIERCE,G.J. 2001. Remotely sensed mesoscale oceanography and the distribution of *Illex argentinus* in the South Atlantic. *Fisheries Oceanography 10: 207-216.*

WELCH,D.W., WARD,B.R. and BATTEN,S.D. 2004. Early ocean survival and marine movements of hatchery and wild steelhead trout (*Oncorhynchus mykiss*) determined by an acoustic array: Queen Charlotte Strait, British Columbia. *Deep-Sea Research II 51: 897-909.*

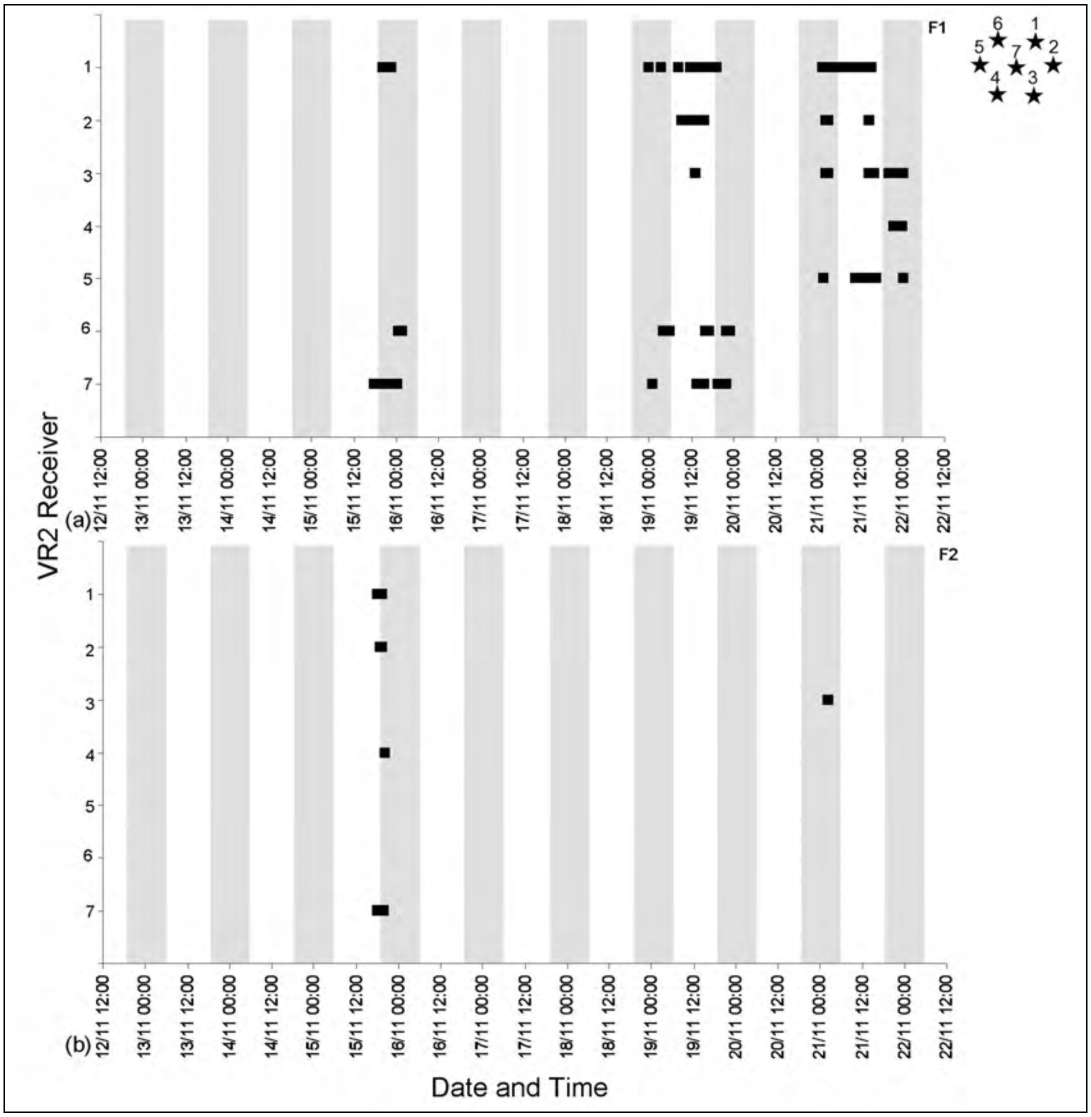
WINDLE,M.J.S. and ROSE,G.A. 2005. Migration route familiarity and homing of transplanted Atlantic cod (*Gadus morhua*). *Fisheries Research 75: 193-199.*

APPENDICES

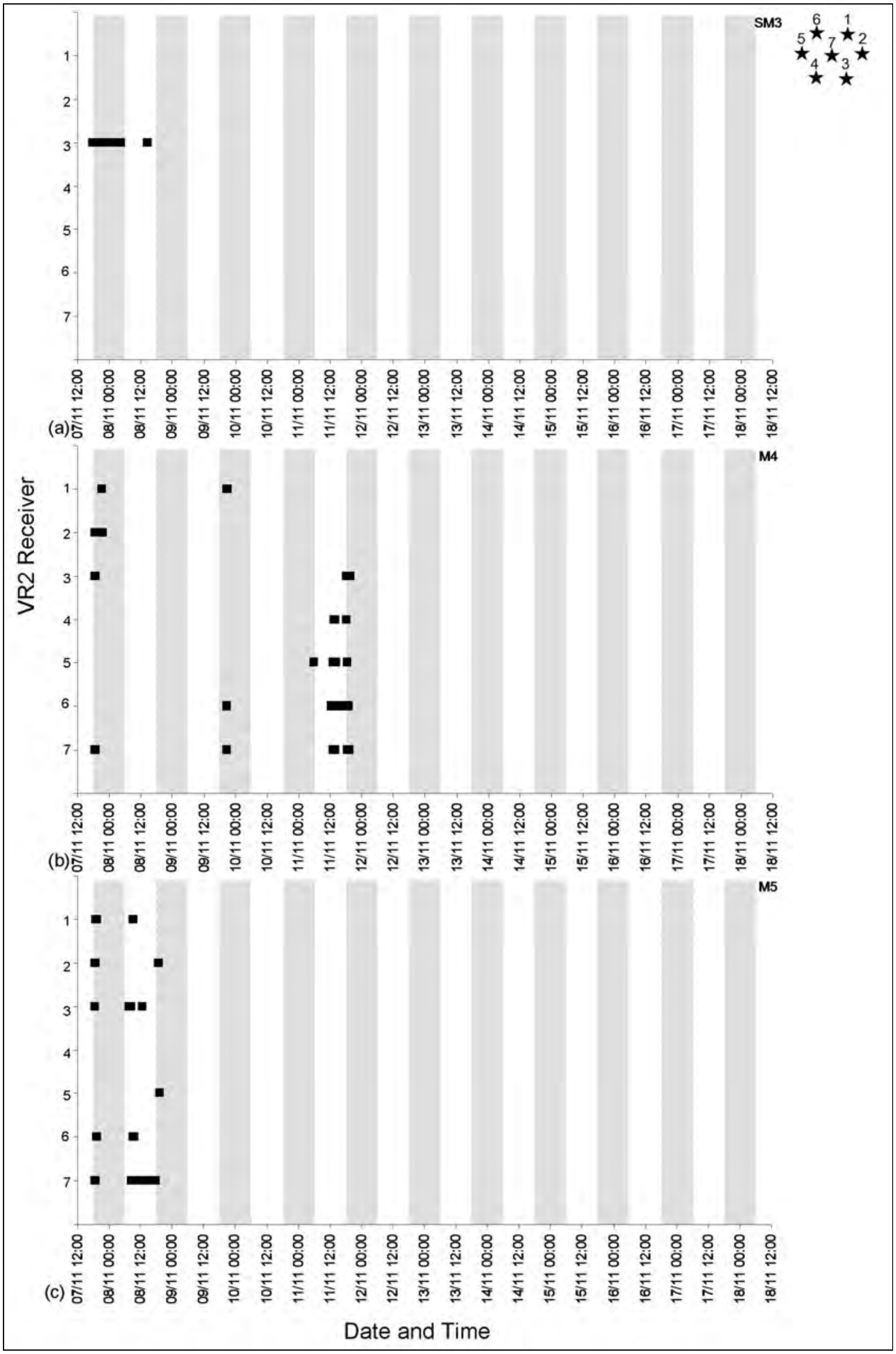
Appendix A1: Spatial occupation of the spawning site over time for the 2003 acoustic telemetry experiment. The VR2 receiver array and VR2 receiver number are also given.



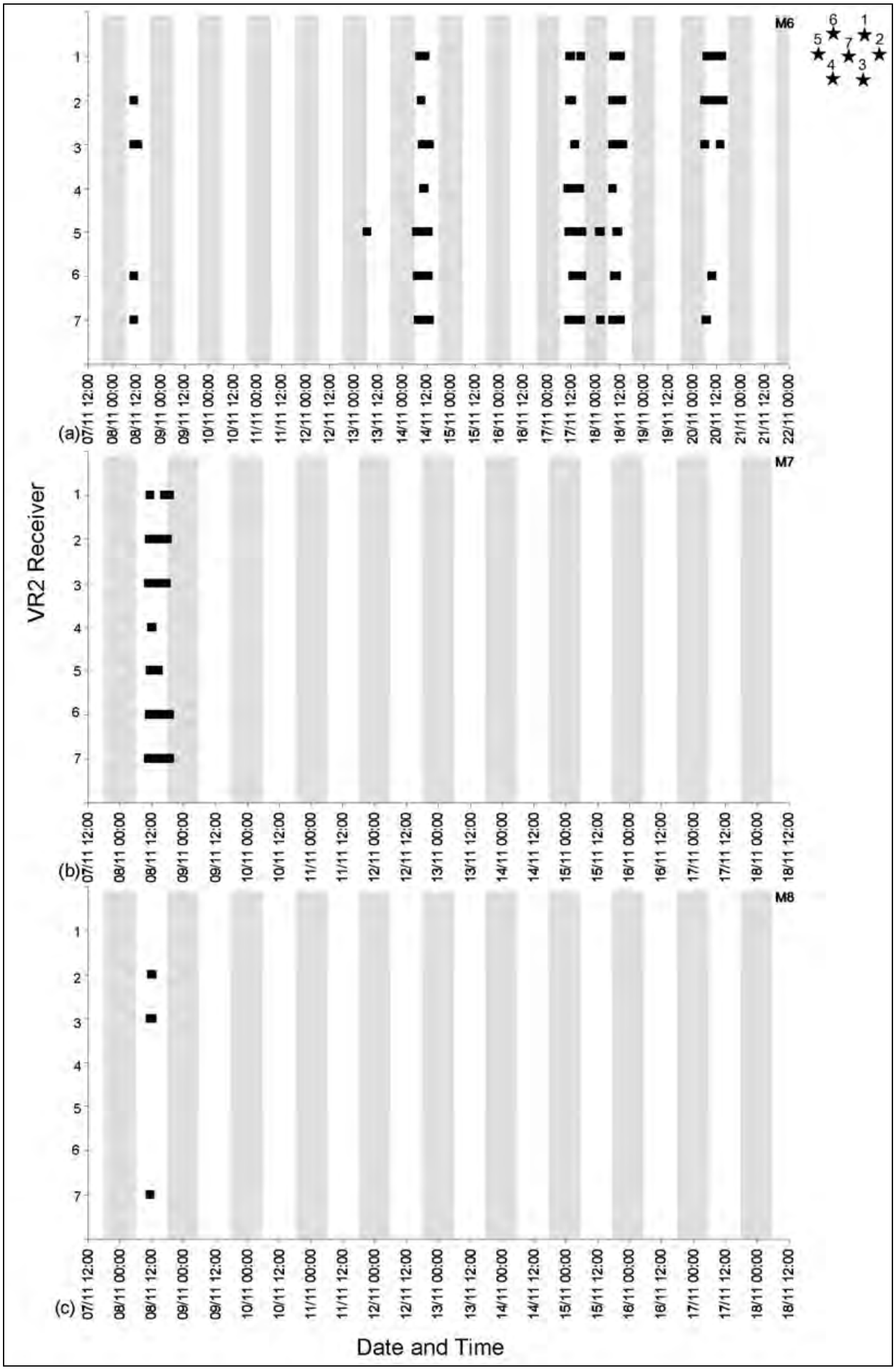
Appendix A1 (cont): Spatial occupation of the spawning site over time for the 2003 acoustic telemetry experiment. The VR2 receiver array and VR2 receiver number are also given.



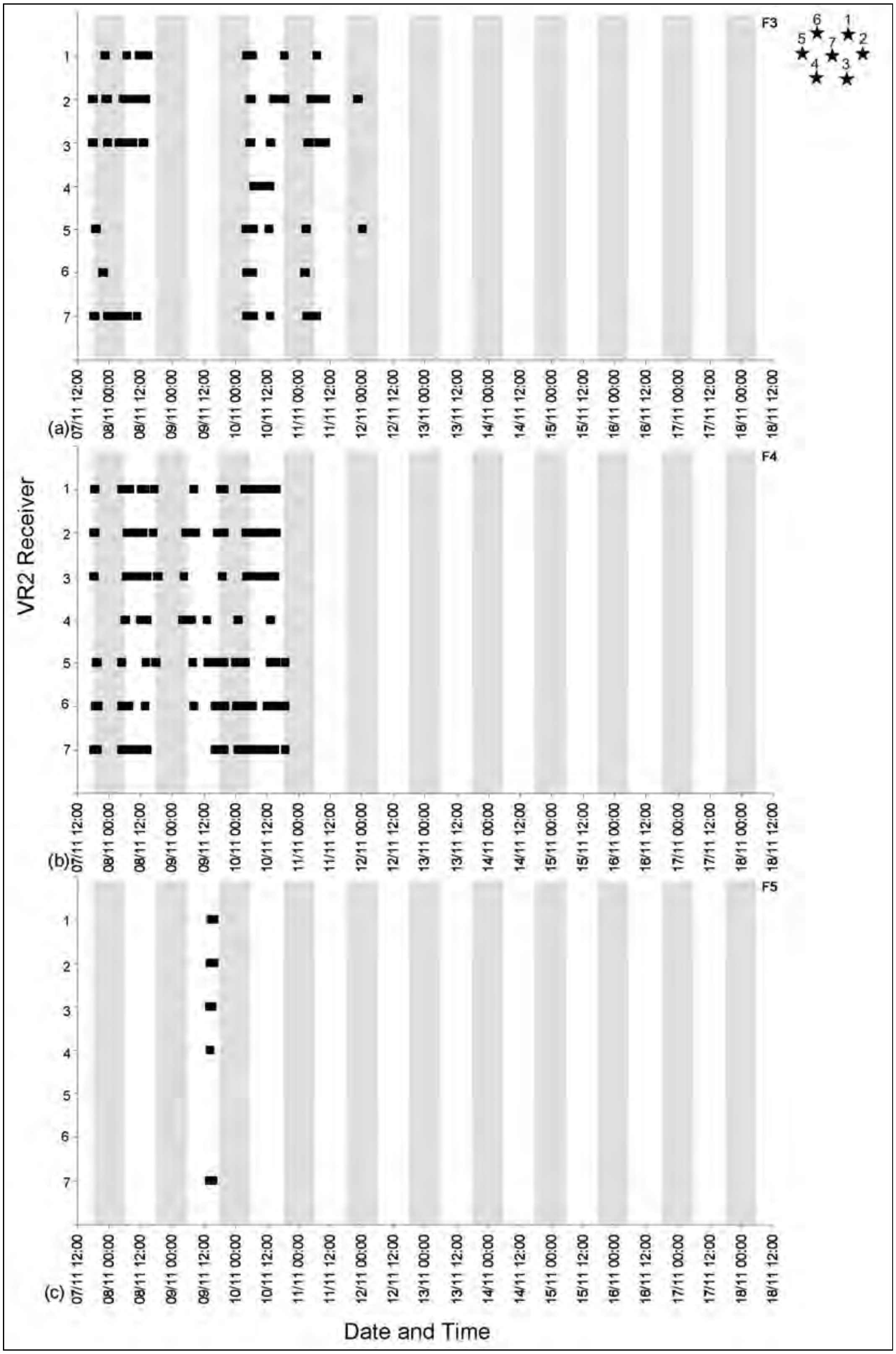
Appendix A2: Spatial occupation of the spawning site over time for the 2004 acoustic telemetry experiment. The VR2 receiver array and VR2 receiver number are also given.



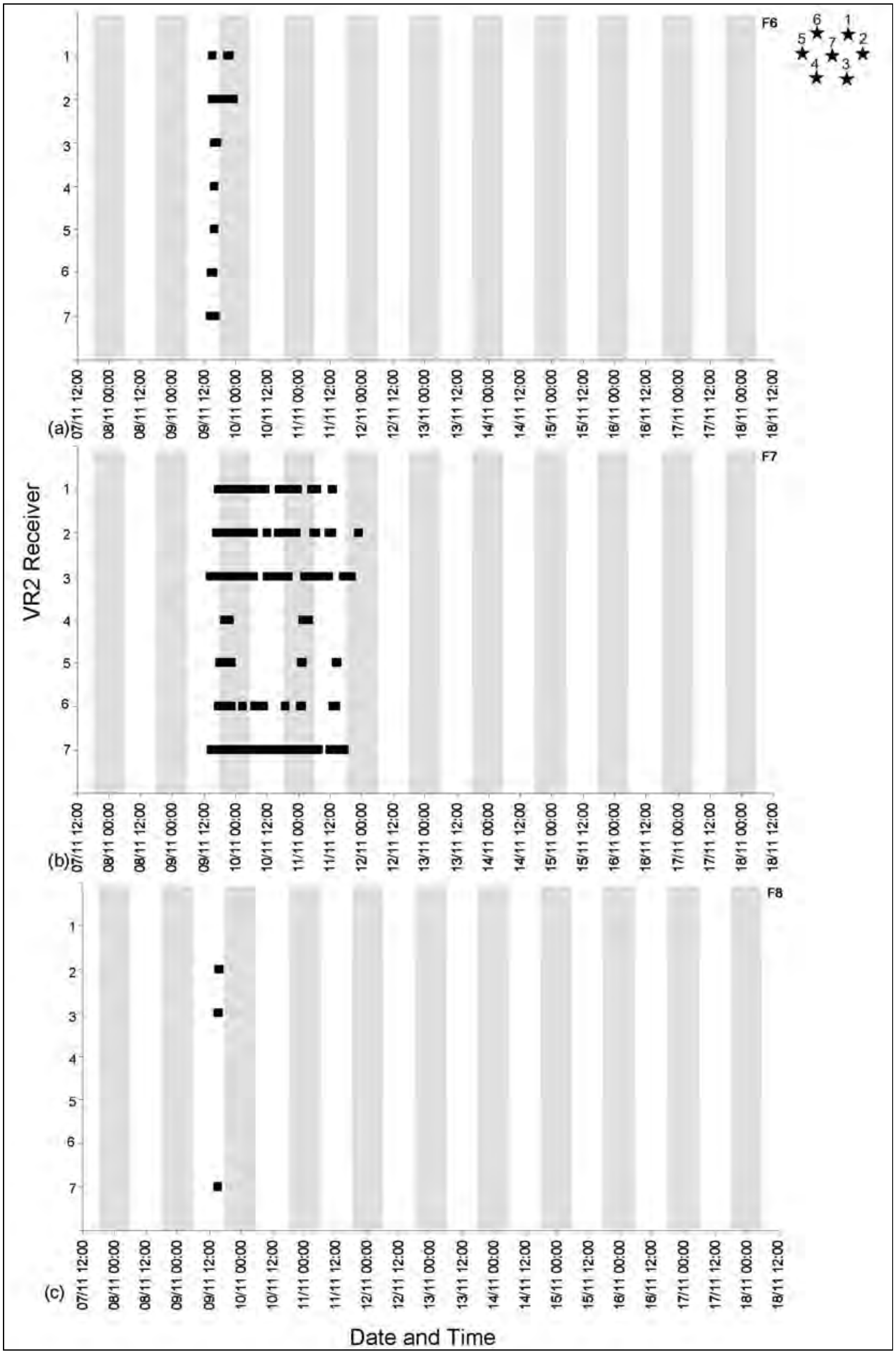
Appendix A2 (cont): Spatial occupation of the spawning site over time for the 2004 acoustic telemetry experiment. The VR2 receiver array and VR2 receiver number are also given.



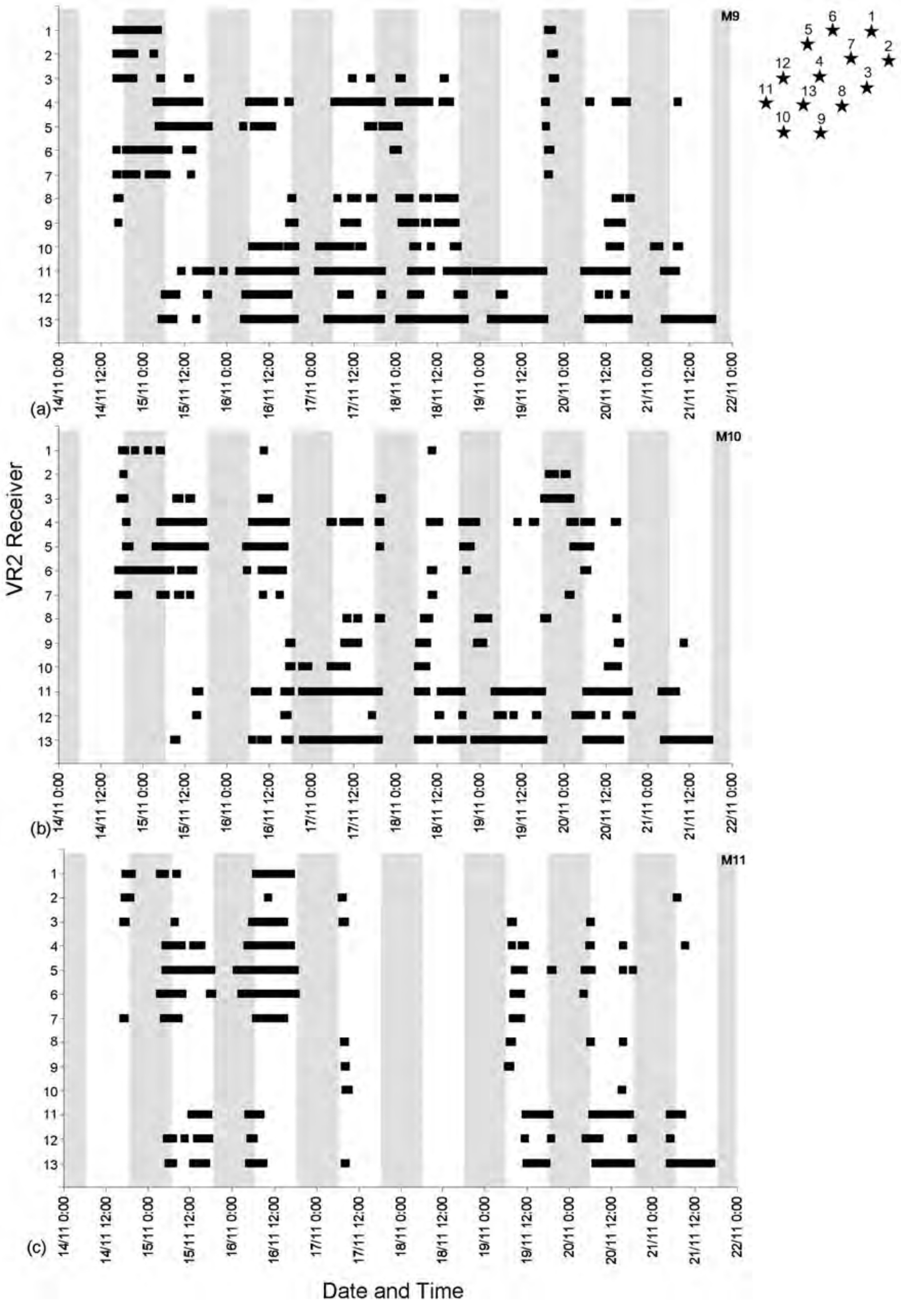
Appendix A2 (cont): Spatial occupation of the spawning site over time for the 2004 acoustic telemetry experiment. The VR2 receiver array and VR2 receiver number are also given.



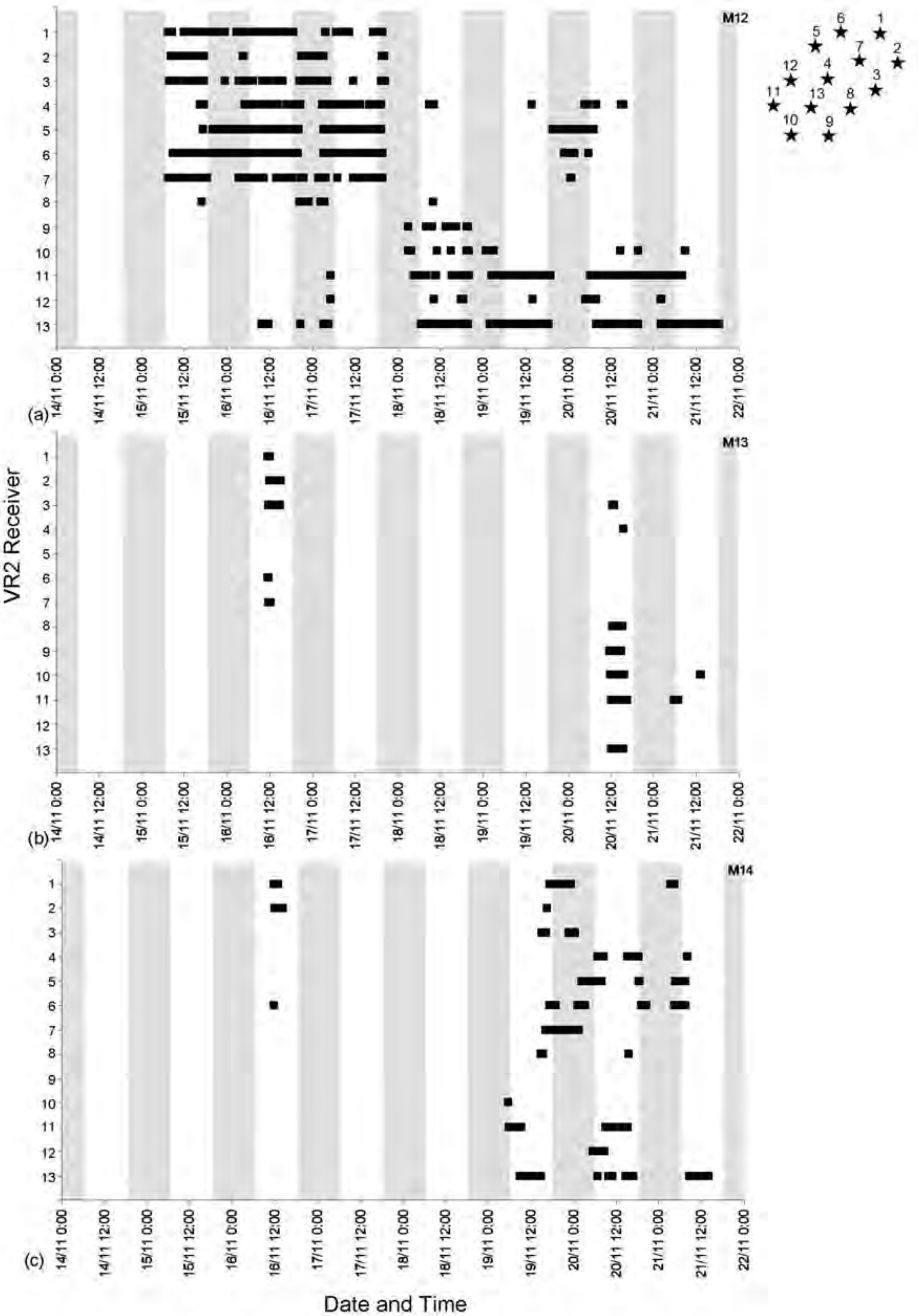
Appendix A2 (cont): Spatial occupation of the spawning site over time for the 2004 acoustic telemetry experiment. The VR2 receiver array and VR2 receiver number are also given.



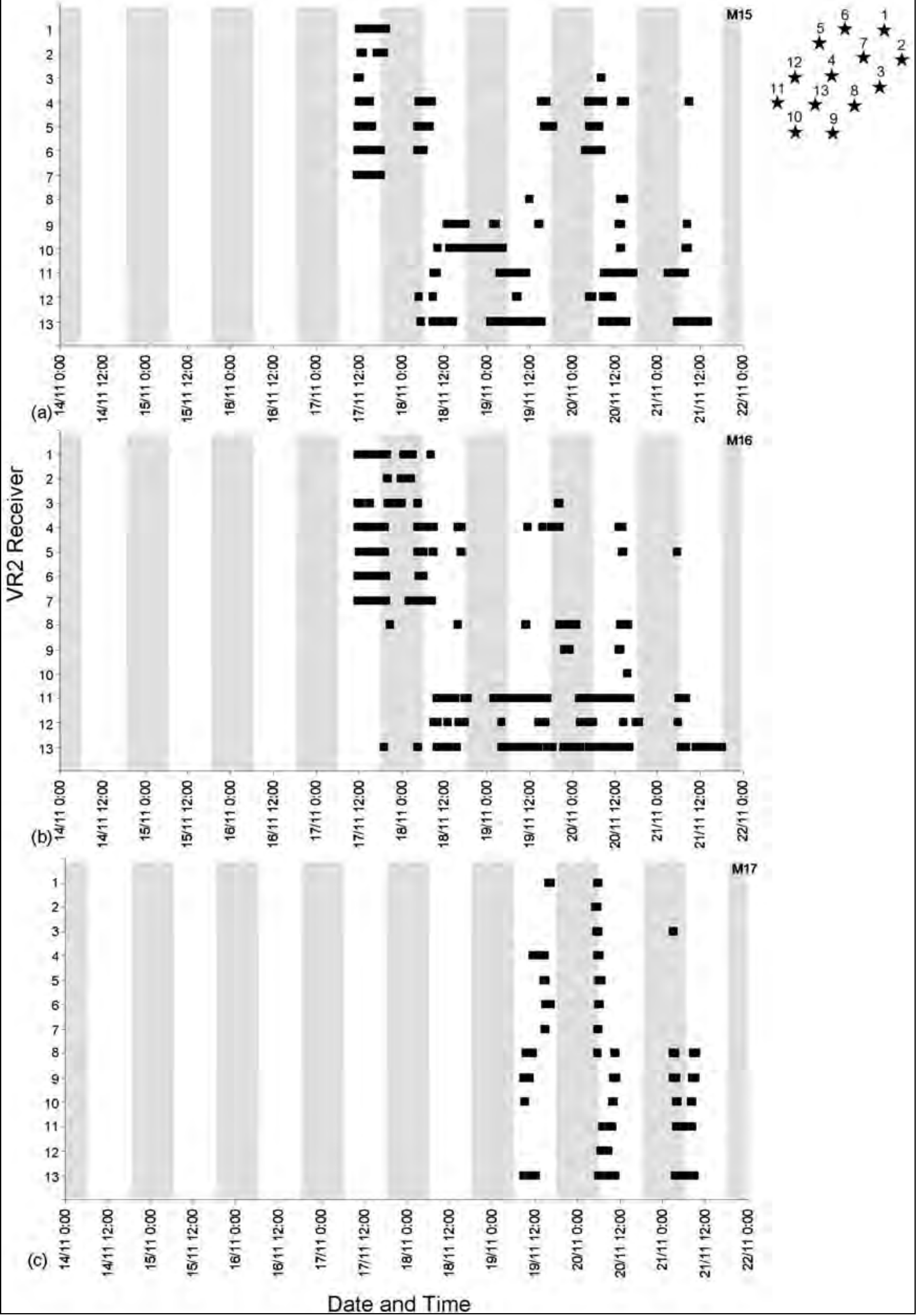
Appendix A3: Spatial occupation of the spawning site over time for the 2005 acoustic telemetry experiment. The VR2 receiver array and VR2 receiver number are also given.



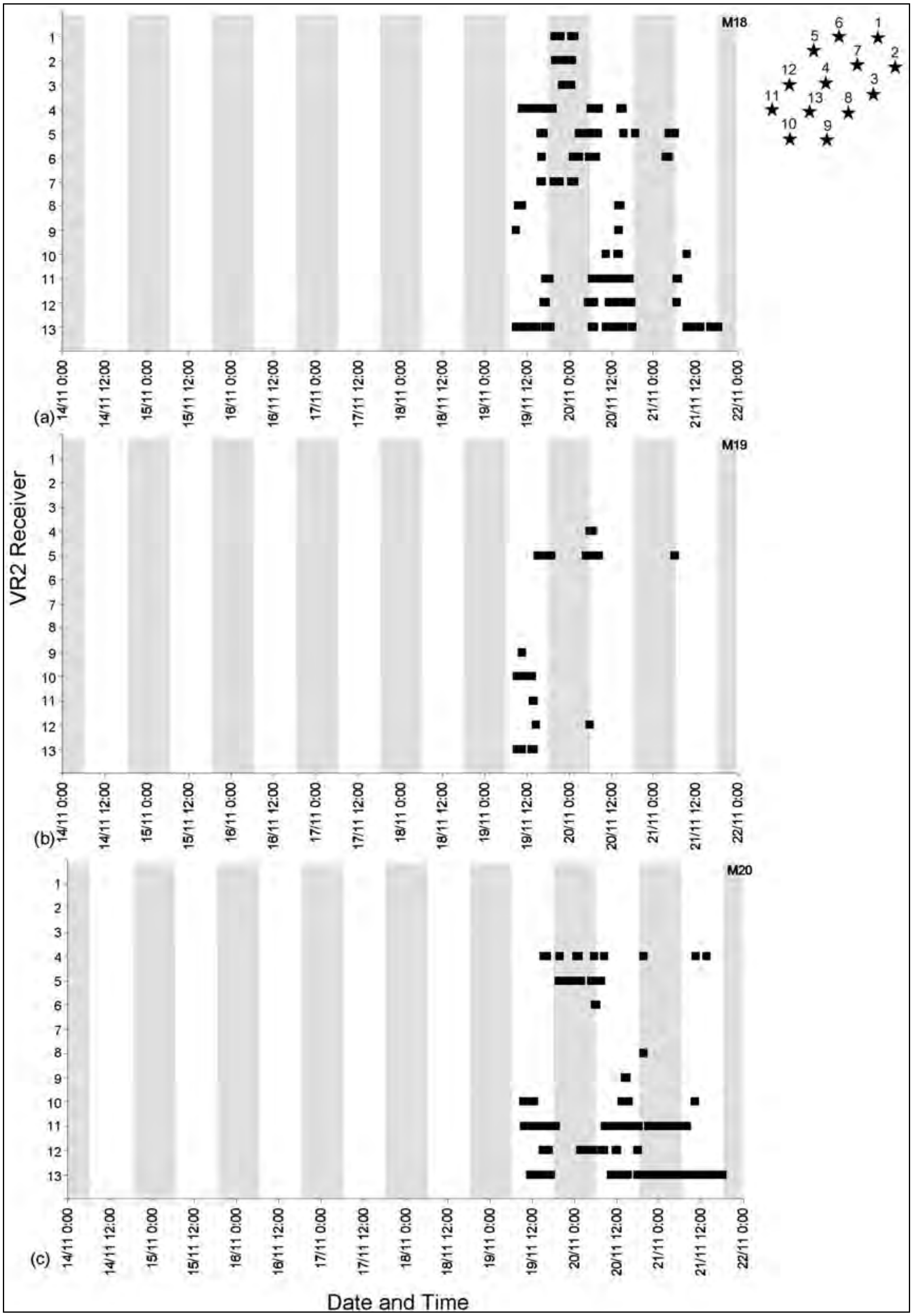
Appendix A3 (cont): Spatial occupation of the spawning site over time for the 2005 acoustic telemetry experiment. The VR2 receiver array and VR2 receiver number are also given.



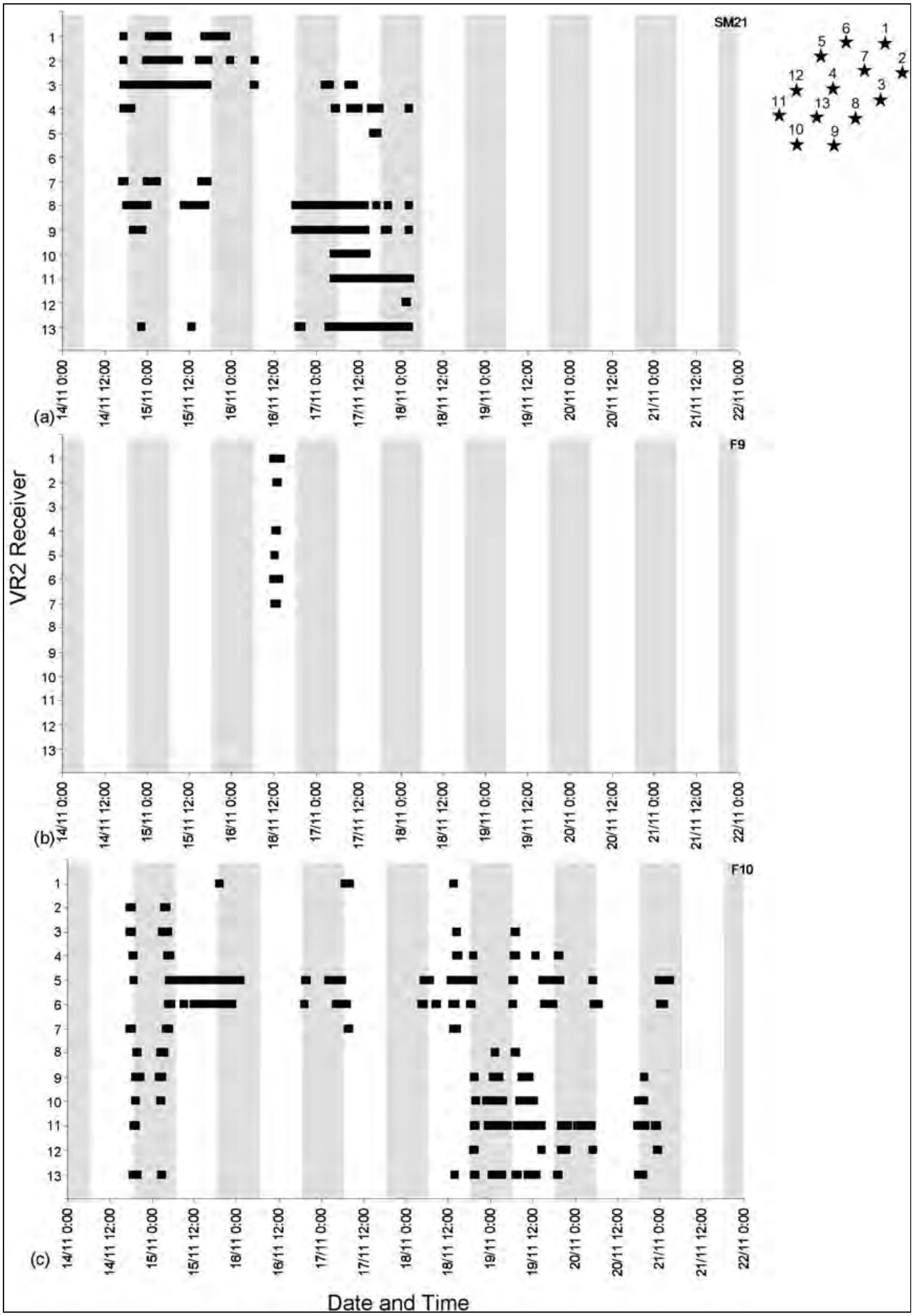
Appendix A3 (cont): Spatial occupation of the spawning site over time for the 2005 acoustic telemetry experiment. The VR2 receiver array and VR2 receiver number are also given.



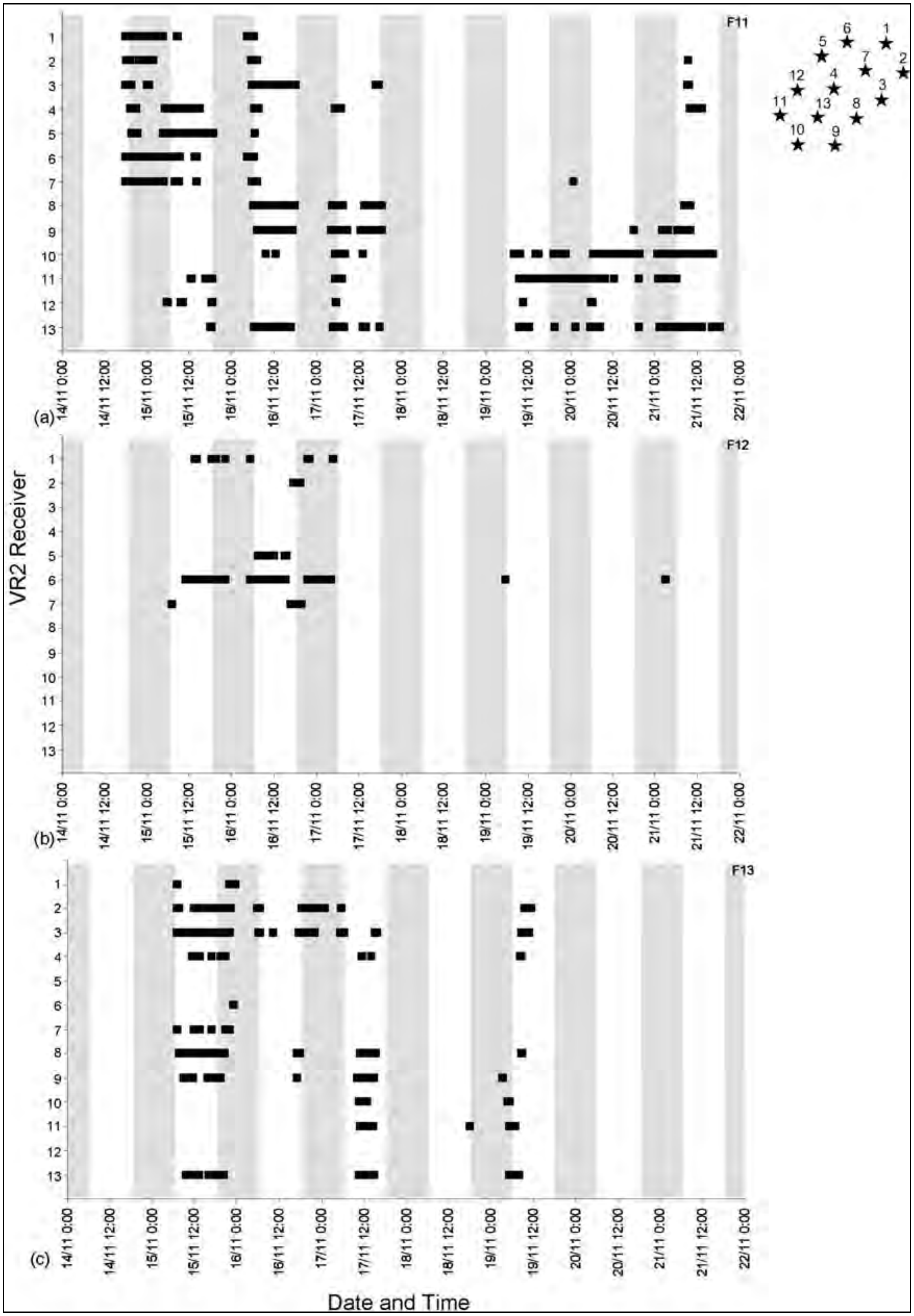
Appendix A3 (cont): Spatial occupation of the spawning site over time for the 2005 acoustic telemetry experiment. The VR2 receiver array and VR2 receiver number are also given.



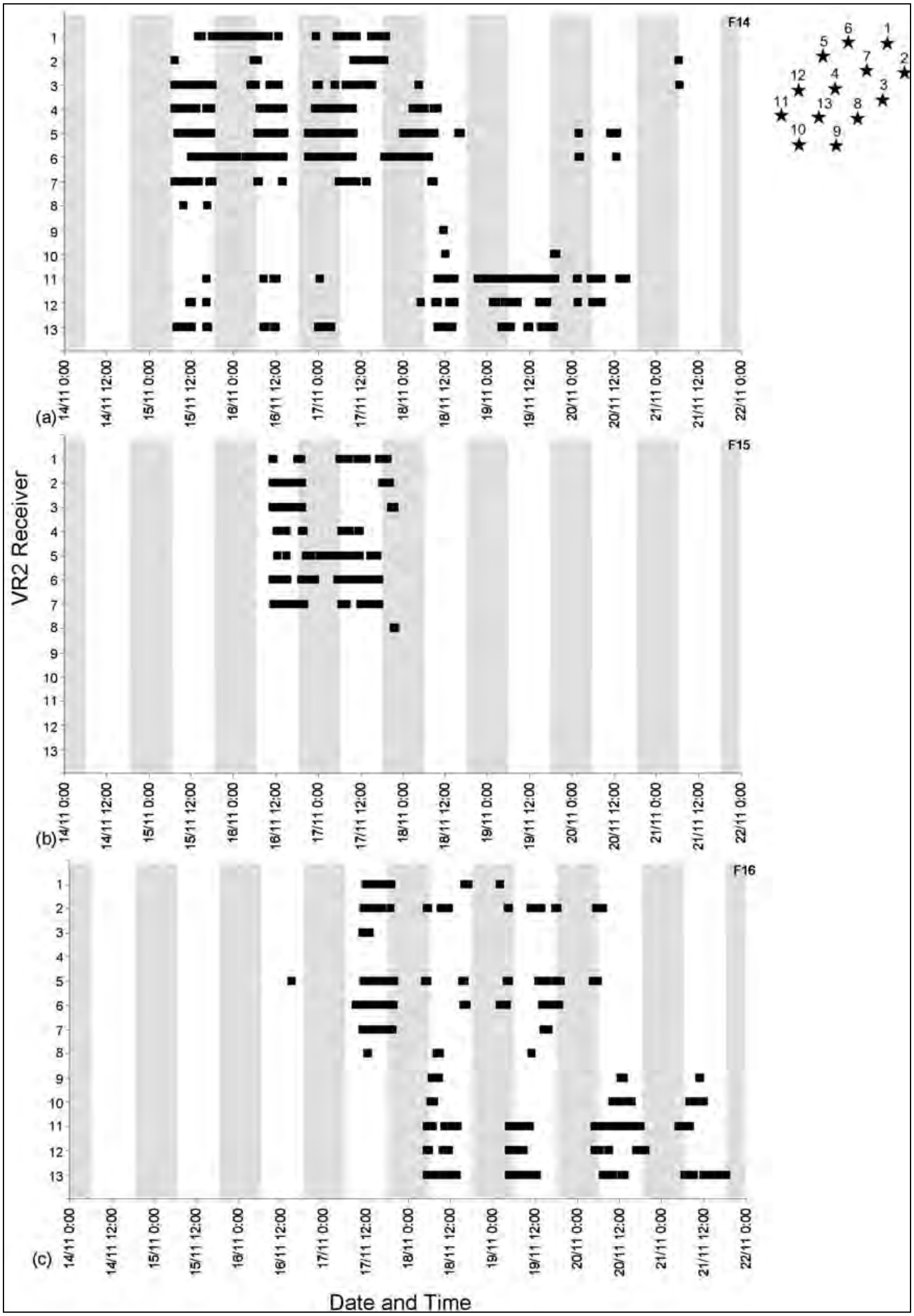
Appendix A3 (cont): Spatial occupation of the spawning site over time for the 2005 acoustic telemetry experiment. The VR2 receiver array and VR2 receiver number are also given.



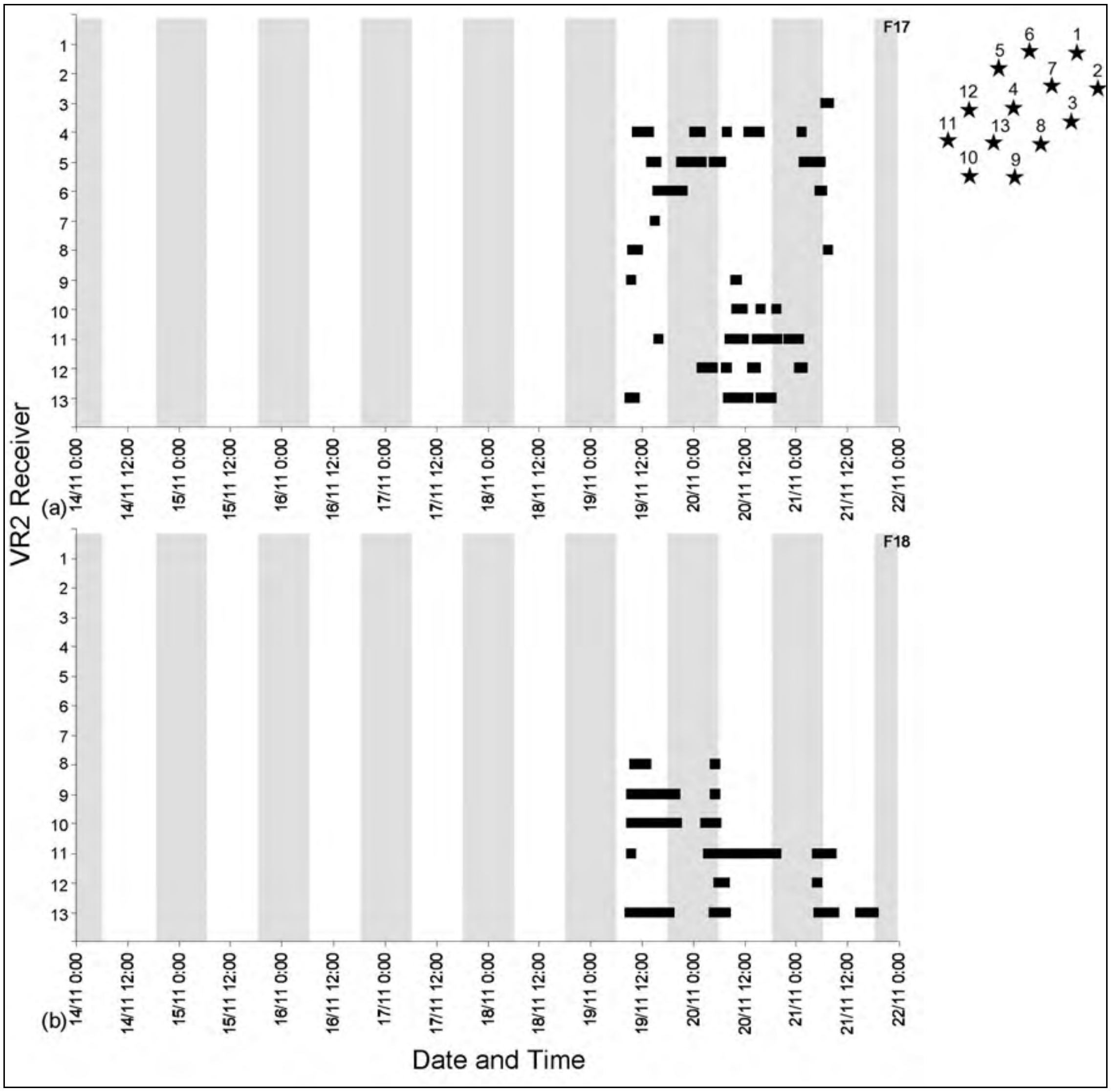
Appendix A3 (cont): Spatial occupation of the spawning site over time for the 2005 acoustic telemetry experiment. The VR2 receiver array and VR2 receiver number are also given.



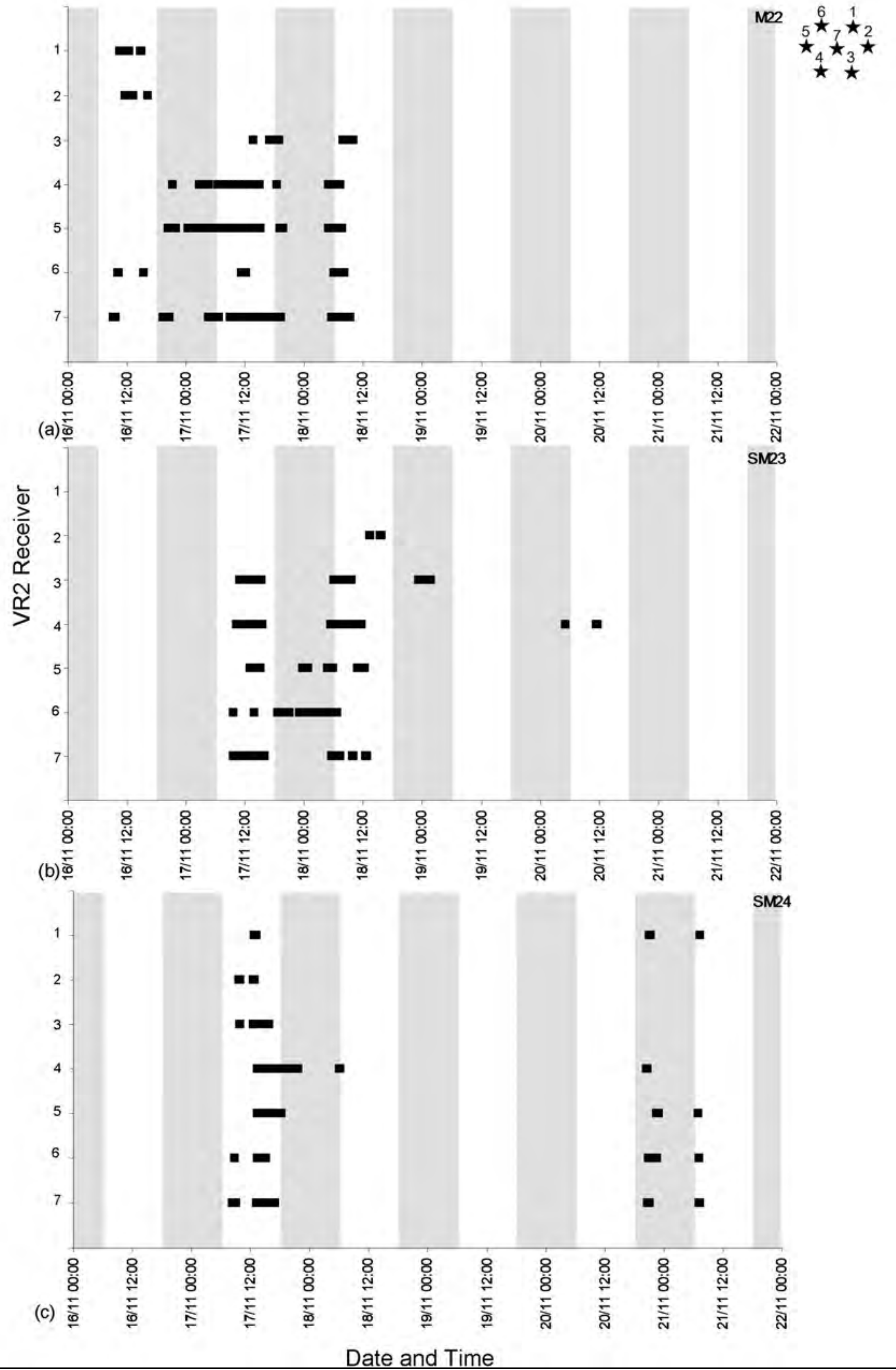
Appendix A3 (cont): Spatial occupation of the spawning site over time for the 2005 acoustic telemetry experiment. The VR2 receiver array and VR2 receiver number are also given.



Appendix A3 (cont): Spatial occupation of the spawning site over time for the 2005 acoustic telemetry experiment. The VR2 receiver array and VR2 receiver number are also given.



Appendix A4: Spatial occupation of the spawning site over time for the 2006 acoustic telemetry experiment. The VR2 receiver array and VR2 receiver number are also given.



Appendix A4 (cont): Spatial occupation of the spawning site over time for the 2006 acoustic telemetry experiment. The VR2 receiver array and VR2 receiver number are also given.