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THE INFLUENCE OF THE ENVIRONMENT ON CHOKKA SQUID *LOLIGO VULGARIS REYNAUDII* SPAWNING AGGREGATIONS: STEPS TOWARDS A QUANTIFIED MODEL

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Published and anecdotal information was used to formulate a conceptual (logic) model which describes the biological components and dynamics of chokka squid spawning aggregations. Into this was integrated potential environmental influences. To determine quantitatively the impact of environmental factors on the spawning process (and ultimately catches), a theoretical methodology was developed based on the use of underwater video images to estimate the rate at which egg pods were deposited. Results from a pilot study undertaken off the Tsitsikamma coast of South Africa demonstrated the viability of this quantitative technique, and while not intended to be a definitive experiment, showed that: (i) an upwelling event was coincident with the formation of a spawning aggregation, supporting the hypothesis that changes in temperature trigger spawning; (ii) biological activities such as egg deposition, predator-induced interruptions in egg deposition, and absence of squid from the egg bed, occupied 19, 22, and 59% of the event time respectively, and (iii) spawning was completed in about 33 h in the absence of female immigration. An overall decline in the deposition rate, combined with the absence of adverse environmental conditions, indicated that spawning was terminated by the ovaries of female squid becoming partially or fully spent, rather than by environmental stimuli. Based on this experience, hardware was then designed and manufactured to realize the methodology, and it is currently being used in a new series of squid spawning experiments.

Forecasting chokka squid *Loligo vulgaris reynaudii* catches and recruitment are goals identified by both fishery managers and the industry (Roberts in prep.). All believe that the environment plays an important role in this regard. However, attempts at finding simple, direct, statistical correlations between readily measurable environmental parameters such as temperature and chokka squid catches have so far failed. This is despite several associations between these data sets (Roberts and Sauer 1994, Roberts in prep.). It would appear that the processes which govern the abundance of squid on the inshore spawning grounds, and hence the jig catches, are more numerous and complex than expected. However, experience gained by the commercial fishing fleet suggests that the abundance of active spawning sites, their size (biomass) and changes in environmental conditions are factors which influence jig catches (and possibly recruitment). Clearly, if progress is to be made towards developing forecasting capability, further investigation of the biological and environmental processes which underpin adult inshore migration and successful spawning is necessary, so that modelling can proceed.

More specifically, work needs to begin on the identification and quantification of the biological components and associated dynamics within spawning aggregations, and to determine interactions with the immediate environment. This paper documents the initiation of this work. First, a conceptual (logic) model of the inshore spawning processes was formulated. Then a theoretical methodology was developed whereby elements of this conceptual (logic) model could be quantified. A pilot study to verify the methodology was undertaken on a chokka squid spawning aggregation off the Tsitsikamma coast of South Africa during November 1995. Based on that experience, hardware was designed and manufactured to support the methodology, and it is currently being used in a new series of experiments. Transforming the conceptual model into a numerical model, supported by an understanding of squid spawning processes, will follow when sufficient data have been collected.

DEVELOPMENT OF THE SCIENTIFIC METHOD

Squid on the spawning grounds

Studies undertaken inshore off the Southern and Eastern Cape using SCUBA and underwater video cameras have shown that chokka squid aggregate when spawning to form concentrations ranging from a few hundred to several thousand individuals (Augustyn 1990, Sauer 1991). The intensity and the duration of these aggregations at specific sites are known to vary considerably over time-scales of

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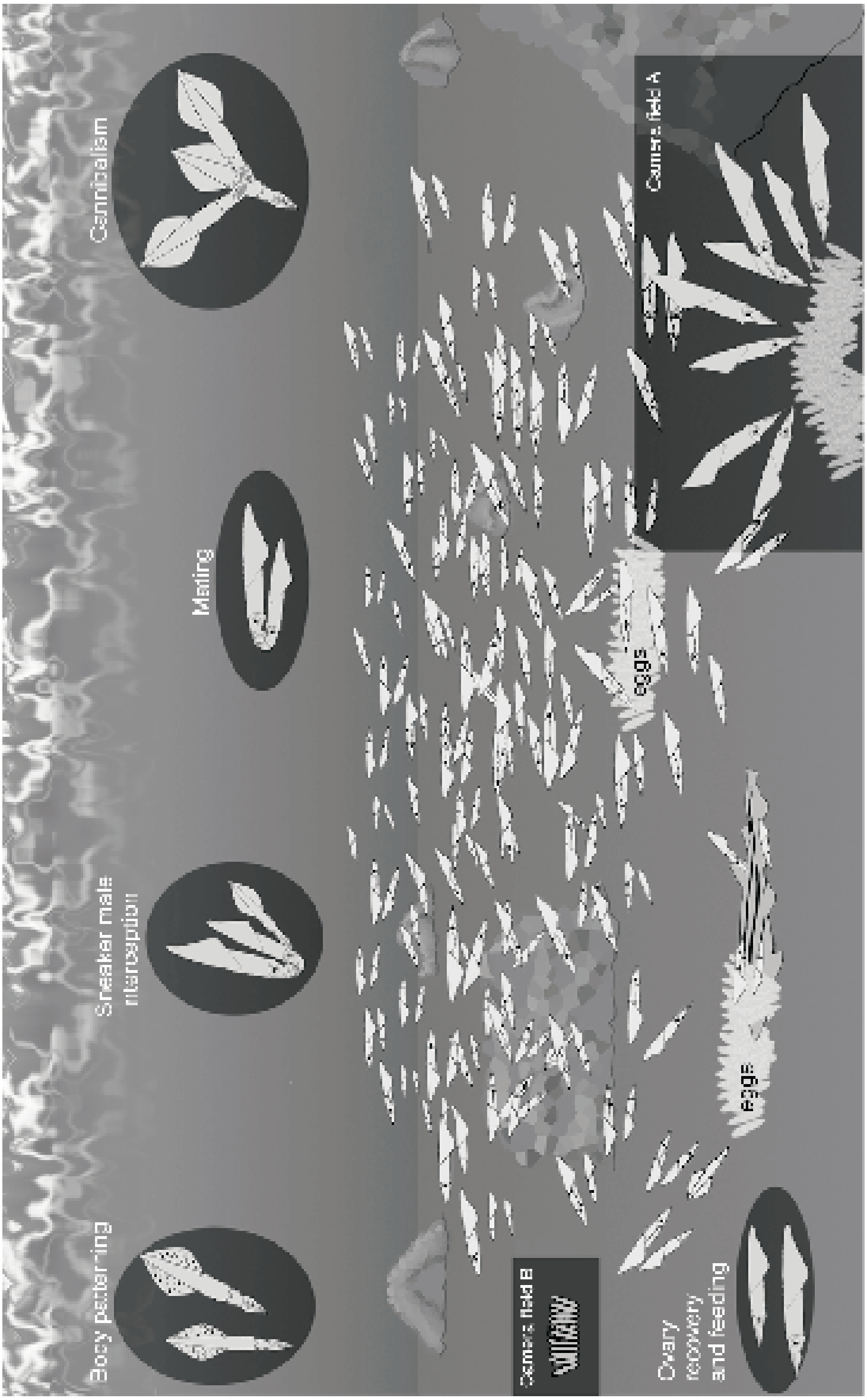

Fig. 1: Schematic representation of a chokka squid spawning aggregation on the inshore grounds, highlighting activities observed during SCUBA dives. The central process is the attachment of egg pods to the substratum

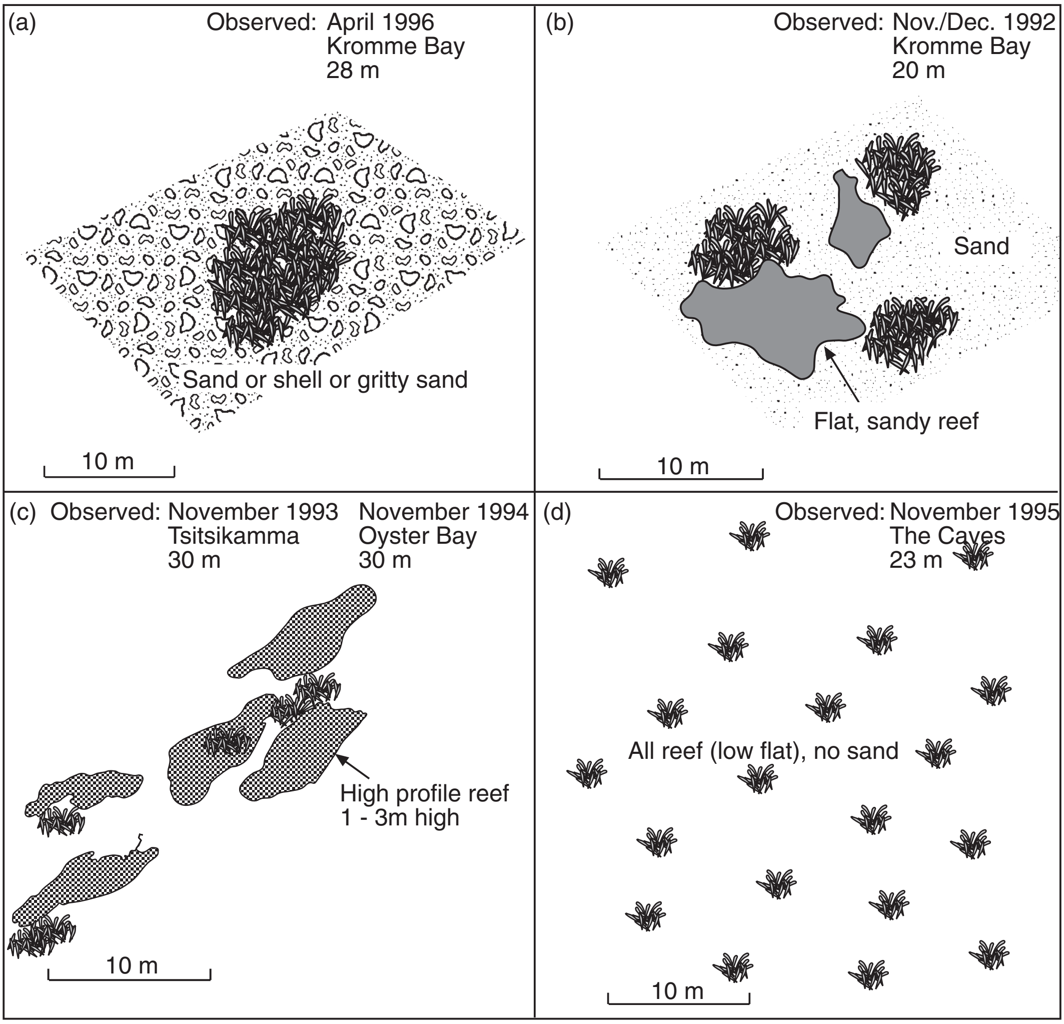

Fig. 2: The "footprint" of chokka squid spawning is the attachment of egg pods to the substratum to form clusters (or beds). Numerous SCUBA diving observations have shown that the layout of egg pod clusters can be classified into the four basic configurations shown here. Note that the sizes of the schematic egg clusters (a–d) are proportional to the 10 m scale

hours, days and months (Sauer *et al*. 1992, Sauer and Smale 1993). Several basic behaviour patterns, schematically depicted in Figure 1, appear to contribute to the spawning process. These include jostling, mating, sneaker male interception, egg deposition (Sauer *et al*. 1993, Hanlon *et al.* 1994), cannibalism and predator avoidance (Sauer and Smale 1991, Smale *et al*. 1995, in prep.). Tagging studies have shown that squid leave and rejoin the aggregation over a 24 h cycle (O'Dor *et al*. 1996, Sauer *et al*. 1997, Lipiński *et al*. 1998), as well as emigrating to and immigrating from other aggregations along the coast (Sauer *et al.* in prep.).

The "footprint" of the spawning process is the cluster(s) of closely packed egg pods (also known as strands or capsules) deposited on the sea floor. Pods are attached to the substratum using an unknown chemical substance. Egg clusters (also referred to as egg beds) conform to the four basic configurations schematically depicted in Figure 2 (Sauer *et al*. 1992,

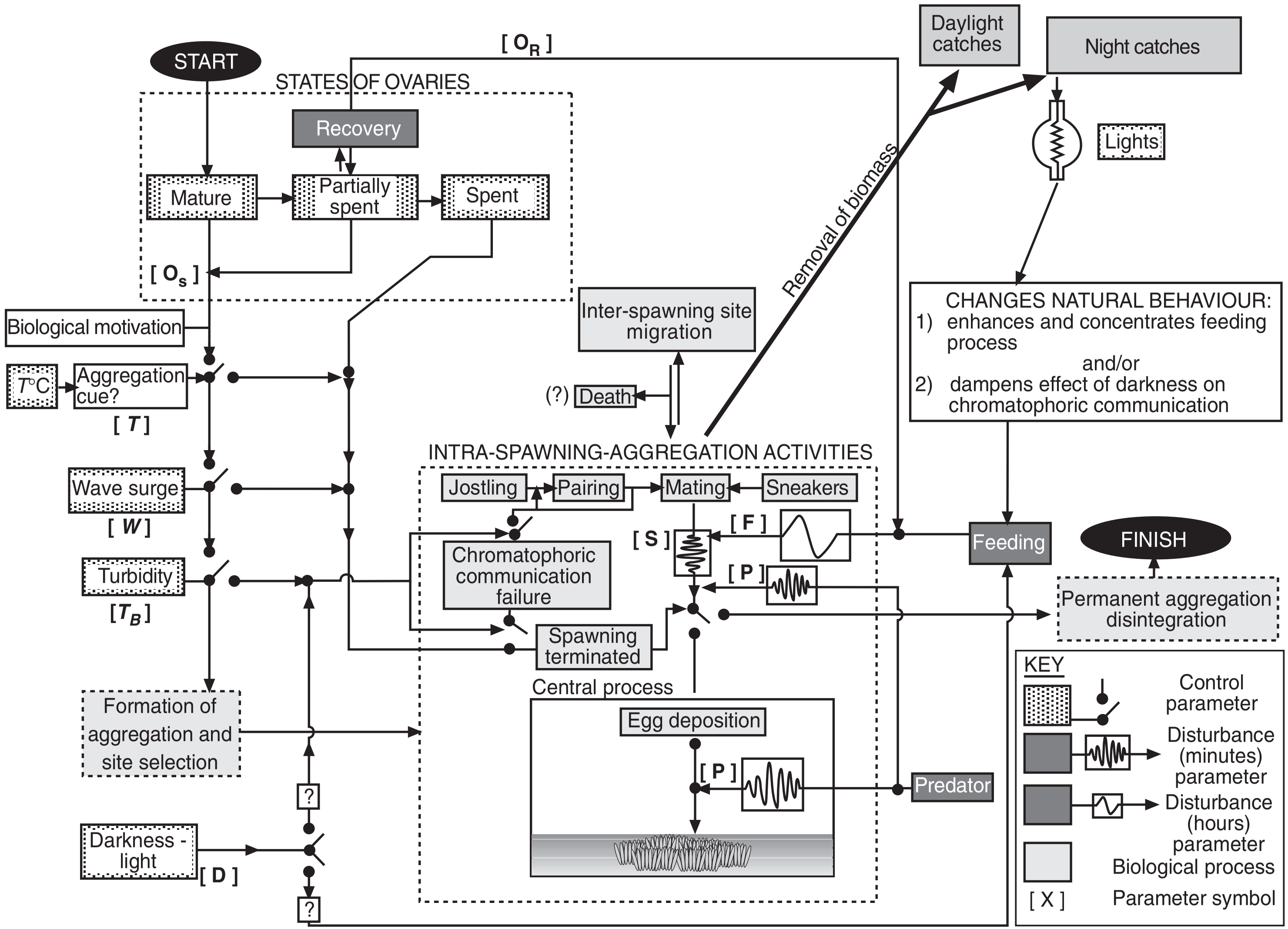

Fig. 3: Conceptual model of the spawning process within a chokka squid aggregation, formulated by combining current biological and behavioural knowledge with potential environmental influences. The ovaries of female squid provide the driving force while environmental parameters control the process by allowing it either to proceed or to terminate. Factors such as feeding, predators, darkness-light and ovary recovery cause temporary disturbances in the spawning process

Roberts unpublished data). No observations to date have been made of egg pods being singly deposited and spread sparsely over an area underlying the squid aggregation (i.e. a total absence of a central egg bed). On occasion, however, single pods have been observed deposited within the surrounds (i.e. <20 m) of an egg bed (Sauer *et al.* 1992, Roberts unpublished information). Pods laid in the shallow coastal regions take approximately four weeks to hatch, depending on ambient water temperature (Augustyn *et al.* 1992, A. Oosthuisen, University of Port Elizabeth, unpublished data).

Conceptual model of the spawning process

Biological knowledge, together with those environmental parameters potentially important (discussed later), were transposed into the conceptual model shown in Figure 3. Essentially, the model consists of four interactive fundamental components. The first of these describes reproductive states of the ovaries for a spawning cohort of female squid, and is considered the primary driving force behind spawning aggregations (and this model). Details of ovary development and functioning for chokka squid have been determined by Sauer and Lipiński (1990), Melo and Sauer (in prep.) and Sauer *et al.* (in prep.), and it is now confirmed that chokka squid are batch (serial) spawners, with spawning taking place throughout the year (Sauer *et al.* 1991). Details of testis development have been described by Sauer and Lipiński (1990). Squid migrate in schools segregated by sex in the vicinity of spawning sites; mixing of sexes takes place only during spawning (Sauer *et al.* 1992). Moreover, males outnumber females by about 2:1 in these aggregations (Augustyn 1990, Sauer 1991). However, there are no descriptions of the initial interactions between these schools, i.e. which sex initiates aggregation and spawning, and the reproductive ability of males. The extent to which male behaviour and their reproductive ability influence aggregation dynamics remains unclear.

In this model, the mature state of the female is considered the starting point and provides the biological motivation for the formation of a spawning aggregation. In the absence of immigration and emigration, it is reasoned that an aggregation will disperse when the ovaries of the cohort become partially or fully spent. The partially spent state used in this context (Melo and Sauer in prep.) implies that ovaries contain post-ovulatory follicles alongside oocytes in various stages of development, including mature ones. In order to keep this initial model concise and practical, only these three ovary states, recognized in the literature, have been included (i.e. mature, partially spent and spent), but future work will require greater detail, encompassing ovary and hormone dynamics.

For the purpose of this model, an additional "virtual" ovary state (or mode) – referred to here as "ovary recovery"– has been included. From a behavioural point of view, this implies a pause(s) within batch spawning, something noted by several local workers. Little is known about the rate at which females lay egg pods, nor of the time required to complete a spawning episode (batch) or the number of batches released by a single female within a season. Melo and Sauer (in prep.) indicate that oocytes in chokka squid can ripen within hours, enabling a female to deposit thousands of eggs within a day or two. This statement has been corroborated by observations in an aquarium in which female chokka squid spawned twice within 12–36 h, depositing as many as 47 egg pods (i.e. an estimated 6 956 eggs) in the first episode and less than half this in the second (De Wet 1995, Sauer *et al.* in prep.). Those authors also observed that partially spent squid caught on jigs had large numbers of mature eggs in their oviducts, and suggested that jigged squid were going through a "resting" stage. No reasoning has been put forward so far to explain these observed pauses, but bio-energetics and oviducal gland activity may be implicated.

The second fundamental component of the model incorporates the role of the environment in the formation and disintegration of spawning aggregations. Some authors have suggested that site selection plays an important role in this regard (Augustyn 1989, Hanlon and Messenger 1996), but Roberts and Van den Berg (in prep.) have questioned this. The last authors point out that numerous SCUBA and video observations have shown that chokka squid attach egg pods to various particle substrata, as well as to reefs. The only substratum apparently unsuitable for deposition of egg pods is fine mud, of which little exists on the main chokka squid spawning grounds off the Eastern Cape (Birch and Rogers 1973). Sauer *et al.* (1991) and Roberts and Sauer (1994), on the other hand, have suggested that temperature plays a key role in catches and spawning. Although identification of the exact mechanisms remains elusive, this suggestion is supported by studies on *Loligo* and other species where temperature has been shown to affect metabolism (e.g. O'Dor 1982, Segawa 1995), ovary development (e.g. Forsythe and Hanlon 1988, Forsythe 1993, Roeleveld *et al.* 1993) and development of egg pods (e.g. McMahon and Summers 1971, Augustyn *et al.* 1992, A. Oosthuisen unpulished data). Other physical conditions potentially important for aggregation and spawning include bottom currents of low to zero velocity, usually caused by surface swell (i.e. bottom surge), and zero to low levels of benthic turbidity (a function of swell-induced turbulence, substratum type and detritus level).

Some squid species are capable of swimming, using fins only, to speeds of 20–40 cm·s^{-1} (Webber and O'Dor 1986). To attain greater speeds they must use jet locomotion. Bearing in mind that squid need to maintain a degree of spatial stability above the egg bed when depositing their egg pods, it is likely that spawning would be terminated when bottom surge exceeds a certain threshold velocity. Under these circumstances, jet locomotion would be too costly in terms of the bio-energetics (O'Dor *et al*. 1994, Wells and Clarke 1996). Also, it appears that communication via chromatophoric patterns plays an important role in the spawning process of many species (Moynihan and Rodaniche 1982, Hanlon *et al.* 1994, Hanlon and Messenger 1996). Despite squid having well developed eyes, turbidity events may well interfere with intraspecific behaviour and terminate aggregation and spawning (Roberts and Oosthuisen in prep.).

Temperature, turbidity and currents have been included in the model as potentially important environmental factors. All three are integrated by way of "switches", because it would appear that they can either trigger or terminate the spawning process. It should be noted, however, that this "switch" logic may be more appropriate for turbidity and currents than temperature, because the first two factors directly and rapidly influence behaviour whereas temperature has a less clear relationship with spawning. The correctness of this logic, however, will be addressed once experiments are underway and data are collected.

The central component of the model is the spawning aggregation. Into this unit is incorporated the observed spawning behaviour and activities noted earlier and depicted schematically in Figure 1. Chromatophoric communication has been included because it is apparently essential for pairing, mating and egg deposition (Moynihan and Rodaniche 1982, Hanlon *et al.* 1994, Hanlon and Messenger 1996).

The fourth component, referred to as "disturbance" parameters, consists of those factors capable of causing a temporary disturbance to the spawning process, most notably the process of depositing egg pods. Two types of disturbance parameters exist: those which cause a temporary disturbance of the order of several seconds to possibly minutes (i.e. predation), and those which disturb the spawning process for several hours (e.g. feeding and ovary recovery). Icons have been used in the model to distinguish between these two types of disturbance.

At present, it is not clear how to integrate the activities of spawning site emigration and immigration (important?), cannibalism (limited importance?) and post-spawning mortality (probably not important). In addition, it would appear that the difference between nocturnal and diurnal spawning behaviour, demonstrated by O'Dor *et al.* (1996) and Sauer *et al*. (1997), could be classified as both control and disturbance parameters: darkness and light are abiotic factors which appear to control the spawning process to a degree, but taken together they do not cause permanent disintegration of the aggregation. However, together they can also be seen as a regular low frequency disturbance parameter. In terms of catches, the darkness-light factor may become important. An acoustic telemetry experiment (O'Dor *et al*. 1996, Sauer *et al* 1997) has shown that males and females move away from the egg beds at night, causing disintegration of the spawning aggregation. The reasons for this are not known, but they may be related to disruption of chromatophoric communication or for feeding. The chokka fishing fleet uses lights at night (Sauer 1995) in an effort to maintain high catch per unit effort (*cpue)*. It is possible that the artificial light either enhances chromatophoric communication and enables spawning to continue, so maintaining the aggregation, or it may enhance and concentrate otherwise dispersed feeding.

Wavelet behaviour concept

The next step is to quantify the model elements. This will permit the nature (dynamics) and importance of each element to be determined and the interrelationships with other elements, especially the environment, to be elucidated. Measuring environmental parameters such as water temperature, turbidity and wave height (bottom surge) is not difficult, but little is known about how to quantify the biological elements shown in Figure 3. As already mentioned, an experiment on spawning chokka squid using acoustic tag telemetry was carried out during November 1994 (O'Dor *et al*. 1996, Sauer *et al.* 1997). Similar studies have been undertaken on *Ommastrephes bartramii* by Yoshida *et al*. (1990) and Nakamura (1991), and on *Loligo forbesi* by O'Dor *et al*. (1994). The data of O'Dor *et al.* (1996) and Sauer *et al.* (1997) provide quantitative information for male, female and sneaker movement patterns in and out of an aggregation over 24-h periods (e.g. see Fig. 5 later), and they support the current hypothesis on feeding and ovary recovery. Alone, however, this technique is unable to provide sufficient data to quantify the other elements of the

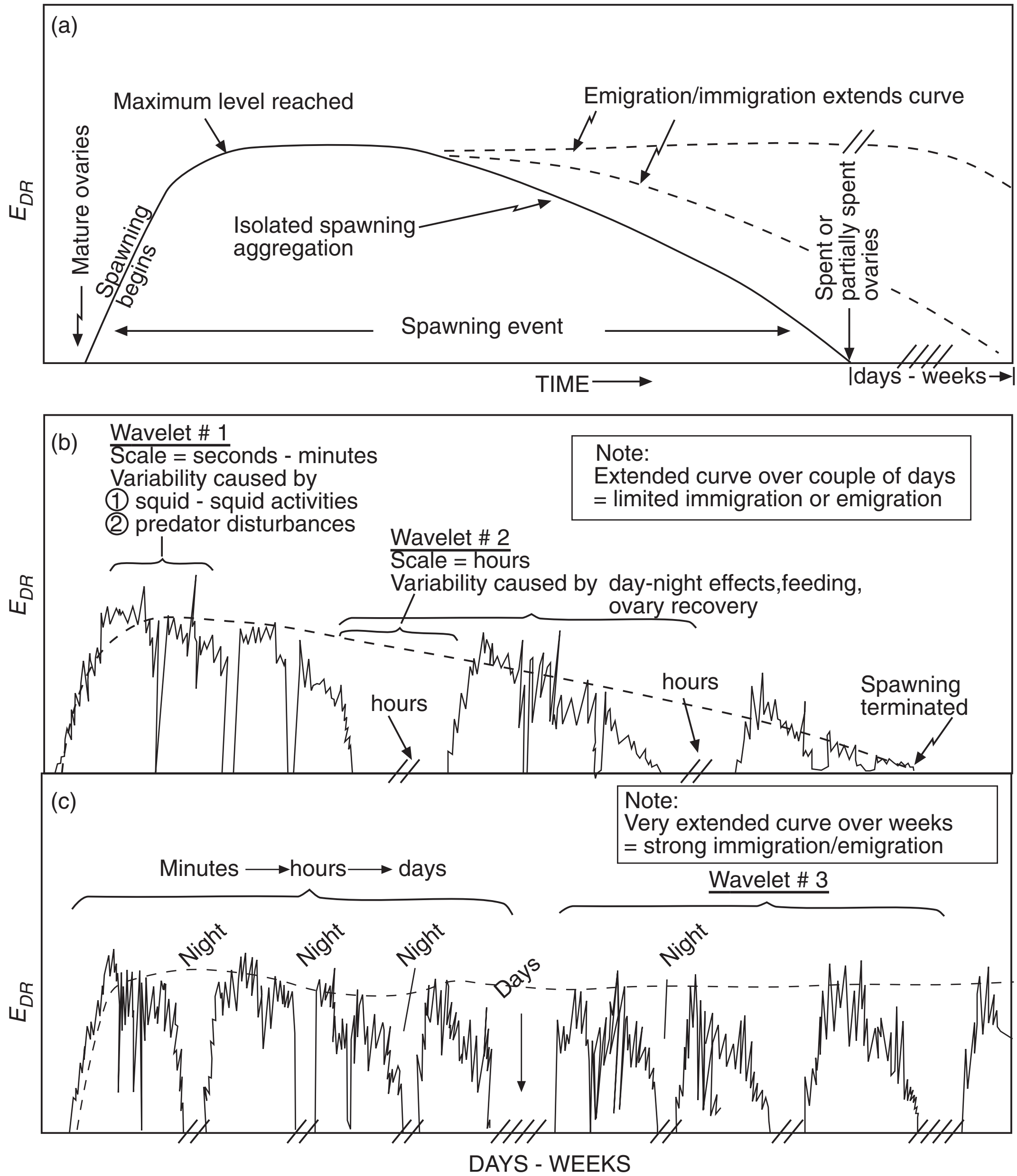

Fig. 4: The wavelet concept used to quantify squid spawning behaviour and the influence of biotic and abiotic factors. (a) Expected curve for egg-deposition rate (E_{DR}) in the hypothetical situation where environmental conditions are favourable and all disturbance factors and immigration/emigration are absent. The effect of immigration of mature female squid is to maintain the E_{DR} for longer periods, i.e. the overall slope decreases. (b) Variability in E_{DR} introduced by factors such as predators, feeding, darkness-light and ovary recovery. (c) Further variability over longer time-scales introduced by environmental factors

model in Figure 3, especially spawning intensity. A more precise indication of the latter is required if any interpretation of the physiological, environmental and disturbance parameters is to be made.

In search of such an indicator, it seems reasonable to begin with the central process of spawning, or egg deposition, because the absolute (total) rate of egg deposition should be related to the intensity of spawning. Furthermore, because squid fishing vessels generally concentrate on spawning aggregations of chokka squid, this indicator should be related to catches. In other words,

$$E_{DR} = f(S) \text{ and } cpue_D = f(S) \quad ,$$

where E_{DR} is the absolute (total) rate of egg deposition (eggs per minute), S the collective term for intensity of mating and associated activities, and $cpue_D$ the daylight catch rate in the aggregation.

Hypothetically, if E_{DR} could be measured over the duration of a spawning event for a large aggregation of squid in a constant favourable environment, and in the absence of all disturbance parameters (i.e. ovary recovery, feeding and predators), darkness-light, and permanent emigration/immigration, then a trend similar to that shown in Figure 4a could be expected. The large numbers of squid, it is assumed, would have the effect of smoothing out perturbations in E_{DR} caused by non-uniform rates of jostling, pairing, mating and other prerequisite egg-deposition activities. Initially, E_{DR} should increase rapidly as the number of squid participating in the spawning process increases. A maximum level, proportional to the size of the aggregation, will be reached. Thereafter, E_{DR} will decline over time as the overall state of the aggregation's ovaries changes from mature to partially spent or spent.

A study by Lipiński *et al.* (1998) indicates that about 20% of an aggregation emigrate each day. Other filament tag experiments (Sauer *et al.* in prep.) indicate that squid emigrate from spawning aggregations and move along the coast to join other aggregations. As shown in Figure 4a, the effect of emigration/immigration on a spawning aggregation will be to maintain the overall state of the ovaries such that E_{DR} is high for long periods compared to cases where aggregations are isolated. High levels of emigration/immigration in a spawning aggregation were observed off Cape St Francis in 1996, when catches were good and spawning continued for three months before final disintegration (pers. obs.)

In reality, it is likely that other factors will come into play. Under these circumstances, E_{DR} is expected to look similar to Figure 4b, seemingly fluctuating on three time-scales, referred to in this paper as "wavelets". The first scale of variability (Wavelet #1) occurs over very short time-periods. These are momentary interruptions to egg deposition which span time-periods ranging from seconds to minutes, caused by squid-squid and predator-squid interactions. The second scale of variability (Wavelet #2), observed over periods of hours, is caused by darkness-light effects, feeding, ovary recovery and predator avoidance. It is thought that the first two factors are related and appear to be *en masse* actions (O'Dor *et al.* 1996, Sauer *et al.* 1997). All factors, in the absence of fishing, involve squid moving away from the spawning site to return several hours later. The third form of variability (Wavelet #3) occurs on a time-scale ranging from days to weeks, and is characterized by a cessation of spawning and total disintegration of the spawning aggregation (Fig. 4c). Anecdotal evidence indicates that spawning sites at times become active again several days or even weeks after the collapse of an aggregation. From the point of view of verifying the influence of water temperature, turbidity and bottom surge, it is this last form of variability in E_{DR} which is of greatest interest.

In summary,

$$E_{DR} = f\,[O_S, \text{Wavelet \#1}(S, P), \text{Wavelet \#2}(D, F, O_R, P_A), \text{Wavelet \#3}(T, T_B, W)\,] \,,$$

where O_S is the overall state of ovaries within an aggregation, P the predator interruptions, D the darkness-light effects, F the feeding interruptions, O_R the ovary recovery, P_A the predator avoidance, T the temperature, T_B the turbidity, and W the wave height.

In terms of the model in Figure 3, these wavelets can be described as follows:

$$E_{DR} = f\,[\text{ovaries } (O_S), \text{control parameters (Wavelet \#3)}, \text{disturbance parameters (Wavelets \#1, 2)}] \quad .$$

Theoretically, these wavelets (and parameters) can be measured by placing an underwater video camera in front of a newly started egg bed (see Fig. 1, Field A), and the number of egg pods deposited can be counted per unit of time. Practically, however, the technique has limitations. First, the E_{DR} discussed above referred to an ideal, absolute quantity in which all eggs deposited per unit of time are counted. In reality, a camera has a field of view which may not monitor the entire egg bed and hence the whole spawning aggregation. Examples of this situation can easily be found when considering the egg-bed configurations shown in Figure 2, mindful that rates of egg deposition differ over the beds and, moreover, that poor underwater visibility will not allow for the total depth of field to be utilized fully. Under these scenarios, the camera is sub-

Table I: Summary of environmental parameters during The Caves (Tsitsikamma) underwater video experiment in November 1995 (depth 23 m, flat reef, start 13:01 on 11.11.95, finish 16:45 on 12.11.95)

Parameter	11 November 1995		12 November 1995	
	Morning	Afternoon	Morning	Afternoon
Wind	SSW gentle breeze	SSW light breeze	NW offshore light breeze	Southerly onshore light breeze/air
Swell	Small, <0.5 m	Small, <0.5 m	1–1.5 m	1–1.5 m
Ground swell impact on eggs	Small but noticeable	Small but noticeable	High	High
Underwater visibility surface/ midwater	5 m	5 m	5 m	5 m
Underwater visibility bottom	8–10 m	7 m	5–7 m	5 m
Temperature near surface	19°C	19°C	19°C	19°C
Temperature bottom	15.5°C	16.5°C	19°C	19°C

sampling and the resultant measured egg-deposition indicator could indicate, prematurely, that spawning within the aggregation had terminated (e.g. Fig. 1, Field B). These problems could be addressed using several cameras, but such action may not solve the subsampling problem. Relocating a single camera to the active areas is not desirable because this would affect the magnitude of the measured indicator and cause discontinuities in the dataset. The multi-camera option is preferable because it allows an average rate of egg deposition to be calculated that is more robust to the microdynamics of spawning.

A further consideration is that it is usually not possible to witness the physical deposition of an egg pod by a female squid. Instead, the observer sees the female squid, paired with the male, swim down to the egg mass and partially disappear in it as she attaches the pod to the substratum (and to other pods). The pair then retreat. At times females are skittish because of the presence of predators or other squid, and retreat without depositing the pod. In creating an indicator of spawning intensity, this is not a problem, because the need is not so much an accurate measure of pods deposited, but rather of the activity.

For these reasons, it is not strictly correct to use the symbol E_{DR}. Rather, in acknowledgement of the limitations outlined, an *Aggregation Intensity Index* (*AII*) will be used, with the assumption that

$$AII = E_{DR} \quad .$$

High turbidity may also interfere with this visual technique and, obviously, it will not be possible to generate a realistic *AII* under such conditions. Although little can be done to determine the rate of egg deposition, there are several technologies that can, in principle, be used to provide proxy data under turbid conditions. Two such technologies are high resolution digital imaging sonar and three-dimensional acoustic telemetry, the latter already proven and used on chokka squid (O'Dor *et al*. 1996). In the case of acoustic telemetry, for example, should all tagged squid leave the spawning site during a turbidity event, then it can be concluded that *AII* is zero.

Finally, the wavelet method alone will not allow all the biological parameters shown in Figure 3 to be measured quantitatively. Predator interruptions P in the vicinity of the egg beds can be counted directly on video, but the remaining parameters will require other technologies integrated with the visual imagery. Parameters D and F, for example, can be quantified using acoustic telemetry (O'Dor *et al*. 1996, Sauer *et al*. 1997), but they will also require biological sampling. Of great importance is to find methods whereby O_S and O_R can be distinguished and monitored quantitatively. Without this information it is not possible to separate the effects on spawning behaviour caused by environmental or ovary changes.

PILOT STUDY: MEASURING THE AGGREGATION INTENSITY INDEX USING UNDERWATER VIDEO

Site, method and analysis

An inexpensive, standard, monochrome, closed circuit, 430-line video camera (Panasonic) was placed in an underwater housing, which in turn was mounted on a metal frame 50 cm high. The apparatus was deployed during the closed season for squid fishing (i.e. November) in 1995, on a newly started egg bed 23 m deep, 2 km from the coast, and opposite a landmark known as The Caves. The substratum consisted of a flat reef with no sand patches. The small size of the isolated clusters of egg pods (10–15 cm) indicated that spawning had begun a few hours prior to the ship's arrival at midday. The clusters were spread over an area of sea floor in excess of 100 m^2 (Fig. 2d). Immediately, SCUBA divers positioned the video camera 2 m in front of one of these egg clusters. The video signal was transmitted via a 200 m coaxial cable to a monitor and VHS video recorder aboard an anchored commercial chokka-fishing boat. Small floats were attached to lift the cable and to prevent it from snagging the sea floor as the vessel rotated on the anchor. Video recording began at 13:01 on 11 November, and was terminated at 16:45 the following day, when egg deposition had virtually ceased. Over this period the monitored egg cluster had increased in size to 60 cm, but it still remained well within the field of view of the camera. No underwater lighting was used and therefore, after sunset, it was no longer possible to obtain an underwater visual image.

Environmental conditions at the site were monitored and are summarized in Table I. On completion of the deployment, the video tapes were analysed using one minute as the unit of time for counting female squid depositing egg pods and, hence, calculating the rate, i.e. the *AII*. In addition, four other sets of data were generated from the tapes. These were the total time within each minute expended by:

(i) the activity of egg deposition by females (t_{egg}),
(ii) disturbances in the egg-deposition activity caused by predators (t_{pred}), i.e. parameter *P*,
(iii) squid activities other than egg deposition and predator disturbances (t_{bio}), i.e. parameter *S*,
(iv) the longest continuous period (term) of absence from the egg cluster by squid (t_{abs}).

For clarity, these are referred to as "analytical" parameters, distinct from the "control" and "disturbance" parameters in the conceptual model (Fig. 3). It should be stressed that the function of analytical parameters here is to quantify visual imagery and to extract the maximum quantitative data from the video tapes. Individually, they may not necessarily resolve model parameters directly, but collectively, and coupled with other sampling, may improve understanding of the dynamics within spawning aggregations.

Results

The main result of the analysed video tapes, the *AII*, is shown in Figure 5. The form of the plot is similar to the theoretical curve in Figure 4, with Wavelets #1 and #2 evident, as well as Wavelet #3, if it is assumed that spawning terminated soon after the camera was recovered. This demonstrates that it is possible to measure the *AII* and, moreover, that the theoretical understanding of the processes described in this paper is probably correct. In this case, the *AII* for the first 6 h of the experiment was characterized by rapid fluctuations on a time-scale of minutes. At the onset of darkness, the *AII* dropped rapidly in magnitude to a low level. In the absence of lights it was not possible to observe whether spawning ceased completely during the hours of darkness. However, the results of the acoustic experiment of O'Dor *et al.* (1996, reproduced in Fig. 5) indicate that this was probably the case. At sunrise the following morning, the increase in *AII* indicates that spawning resumed, but not at the same consistent rate as on the previous day.

As already indicated, the analytical parameters t_{pred}, t_{bio} and t_{abs} permit considerable quantitative information to be extracted from the video tapes. This information helps to resolve the model parameters *P* and *S*, and indirectly contributes to determining O_S (and O_R), *F* and P_A. As expected, the *AII* is strongly correlated with egg deposition (t_{egg}, $r^2 = 0.95$). Figures 6a and 6b clearly illustrate the quantitative potential of this technique by magnifying the processes responsible for Wavelet #1, i.e. model parameters *S* and *P*. It was calculated that, over the duration of the study, t_{pred}, t_{bio} and t_{egg} accounted for 22, 59 and 19% of the time respectively. From Figure 6b, it seems that predators re-appear only when squid do (Smale *et al.* in prep. give a more detailed interpretation of these predator data).

These data complement the overall decline of t_{egg} seen in Figure 7 in that there is a general increase in both the term and frequency of absence through this period (see smoothed curve, Fig. 6c). The longest natural absence noted was 19 minutes, observed towards the end of the event. The 21-minute absence near the beginning was caused by SCUBA divers working at the egg bed, as was the 31 minutes the following day. The general decline in the *AII* and t_{egg} indicates that the average state of the ovaries of squid within this aggregation had changed over the duration of the experiment, from "mature" to either the "recovery" or "spent" modes and, furthermore, that little if any immigration took place. This implies that the time taken for this cohort to complete its spawning episode (batch) was approximately 33 h, agreeing with the aquarium observations of De Wet (1995) and Sauer *et al.* (in prep.). As stated in the theory, O_S (and O_R) should be monitored in future experiments so that environmental effects can be distinguished clearly.

At the time of the spawning event, both wave

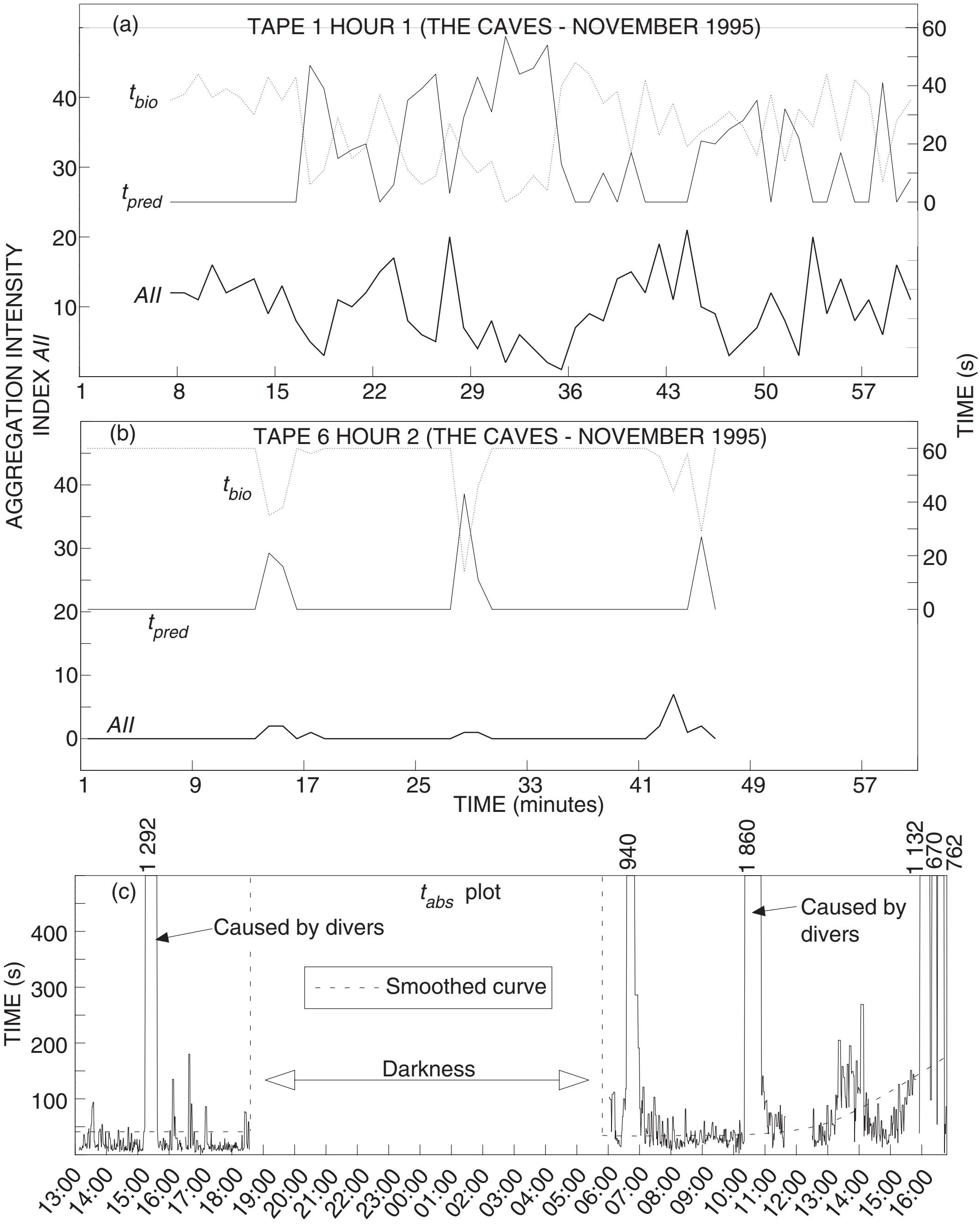

Fig. 6: Video observations of (a) the first hour of study, characterized by many predator disturbances and vigorous egg deposition, (b) the last hour, where egg deposition had almost ceased and the squid disappeared from the field of view. (c) Measure of the longest continuous periods of absence by squid from the cluster during the spawning event (t_{abs})

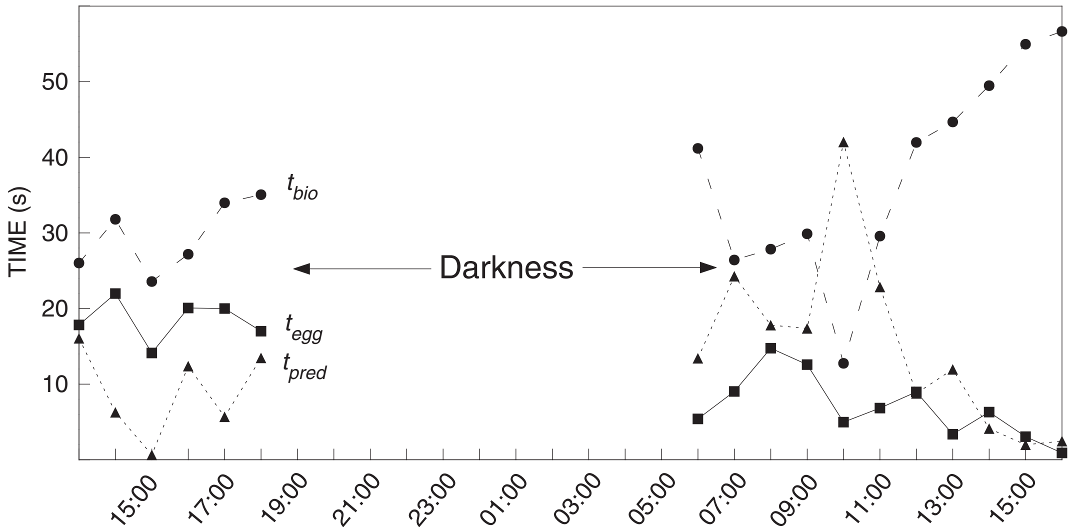

Fig. 7: Hourly averaged data for t_{pred}, t_{bio} and t_{egg}. The slope of t_{egg} (which is highly correlated to *AII*) provides quantitative information on O_S and O_R, as well as on immigration/emigration rates

height (*W*) and turbidity levels (T_B), shown in Table I, were low, and probably had little, if any, influence on the spawning process. In terms of the model shown in Figure 3, this would mean that these two environmental control switches were closed in this particular case, and thereby allowed the aggregation to form. Water temperature, on the other hand, may have influenced the spawning process. The insert plot in Figure 8 shows sea surface temperature (SST) data collected off Storms River some 30 km away. These data serve as an indicator for upwelling (Schumann *et al*. 1995) along the coast. The SST data indicate no upwelling for at least three weeks prior to that pilot study. Despite intensive searches by two commissioned fishing vessels, no spawning aggregations had been found during the three-week period. However, the spawning aggregation studied was found at a time coincident with the first upwelling event, albeit a minor one. As shown in the main plot (Fig. 8), coastal SST at Storms River began to drop at midnight on the evening of 10 November, and by mid-morning the following day, was 13.5°C.

Data collected at the study site itself indicated the presence of a thermocline with a gradient of 3.5°C (Fig. 5). The bottom cooler (15.5°C, and cleaner) layer extended 4 m above the sea floor. Considering the increased size of the egg pod clusters, it was estimated that spawning started early on 11 November 1995. By midnight, the thermocline had disappeared and the bottom temperatures warmed to 19°C, with no apparent direct impact on the *AII* the next day. In view of this, it would seem that the (minor) upwelling event may have triggered the spawning process, although the reason for this is not clear. Furthermore, the overall decline in the *AII*, combined with favourable environmental conditions, indicates that spawning was terminated by the ovaries of the female squid becoming partially or fully spent, rather than by changes in the environment.

In summary, the results from this pilot study demonstrate that video monitoring can be a useful technique in quantifying squid spawning behaviour.

DESIGN AND DEVELOPMENT OF FUTURE HARDWARE

The experience attained in the pilot study has permitted development of a more complex and versatile hardware. Essential elements include a telemetry system which can operate several underwater video cameras remotely, the collection of acoustic data from tagged squid and the supply of continuous environmental data. These data would be transmitted to a shore station for recording. All sea-borne electronics would require indefinite power. The system must be stable at sea, seaworthy, easy to transport both on land and at sea, have minimal interference with the spawning process, and be easy to deploy and recover.

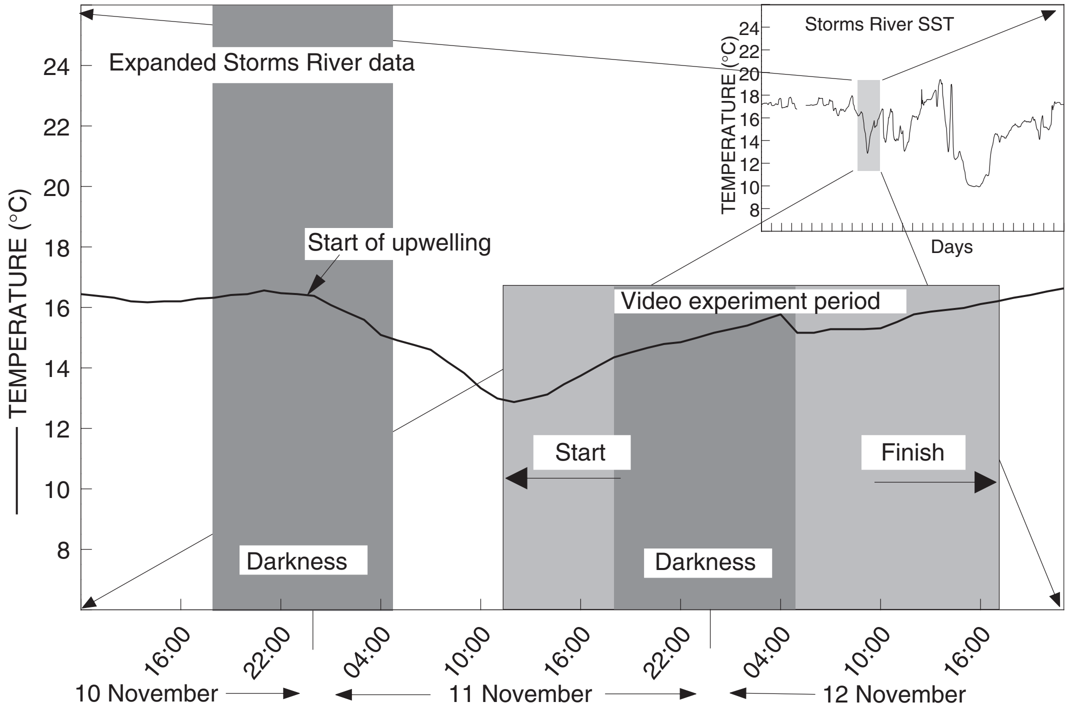

Fig. 8: Sea surface temperature data collected from the nearest monitoring station at Storms River (Tsitsikamma coast), showing the absence of upwelling before the pilot study. The hours of darkness and times of the video study are superimposed. The minor upwelling event which started on the evening of 10 November 1995 may have triggered spawning

Hardware design

The hardware designed and manufactured is shown schematically in Figure 9, where basic components have been emphasized. The design is referred to as UVEATS (Underwater Video-Environmental-Acoustic Telemetry System). Brief specifications can be found in the Appendix.

UVEATS is designed to work on the inshore spawning grounds in depths ranging from 20 to 35 m, and in principle should be capable of transmitting video images and data over distances of up to 10 km. The central unit at sea is a metal surface buoy which functions to supply all electronics with indefinite power, to collect and transmit electronic signals, to identify the exact position of an experimental site, and to keep vessels clear. The size, configuration and construction of the buoy is such that it can operate during storm conditions (i.e. maintain horizontal position and remain stable in the vertical plane). Although the total length is 6.2 m and its mass 450 kg, the modular design (buoy, battery compartments, solar panel frame and mast) allows easy transportation on land and deployment at sea. Modules are assembled onshore and then towed to the site in the horizontal position, using an air bag to float the battery-compartment end of the buoy. This arrangement allows small vessels such as 5–6 m inflatable boats to deploy UVEATS.

The electronics are housed in two separate watertight compartments located in the main buoyancy chamber of the buoy. The entire buoyancy chamber is filled with foam to prevent the buoy from sinking should a leak develop, and to provide insulation for the electronics. Power is supplied by a bank of batteries stored in two separate watertight subsurface cylindrical chambers located at the bottom of the buoy, to lower the centre of gravity. The batteries are capable of supplying power for about 19 days without charging. Charging is by solar energy from three panels positioned geometrically on the superstructure. Buoyant cables connect the surface electronics with the seafloor instrumentation and video cameras. These enter the water via a central duct to prevent entanglement

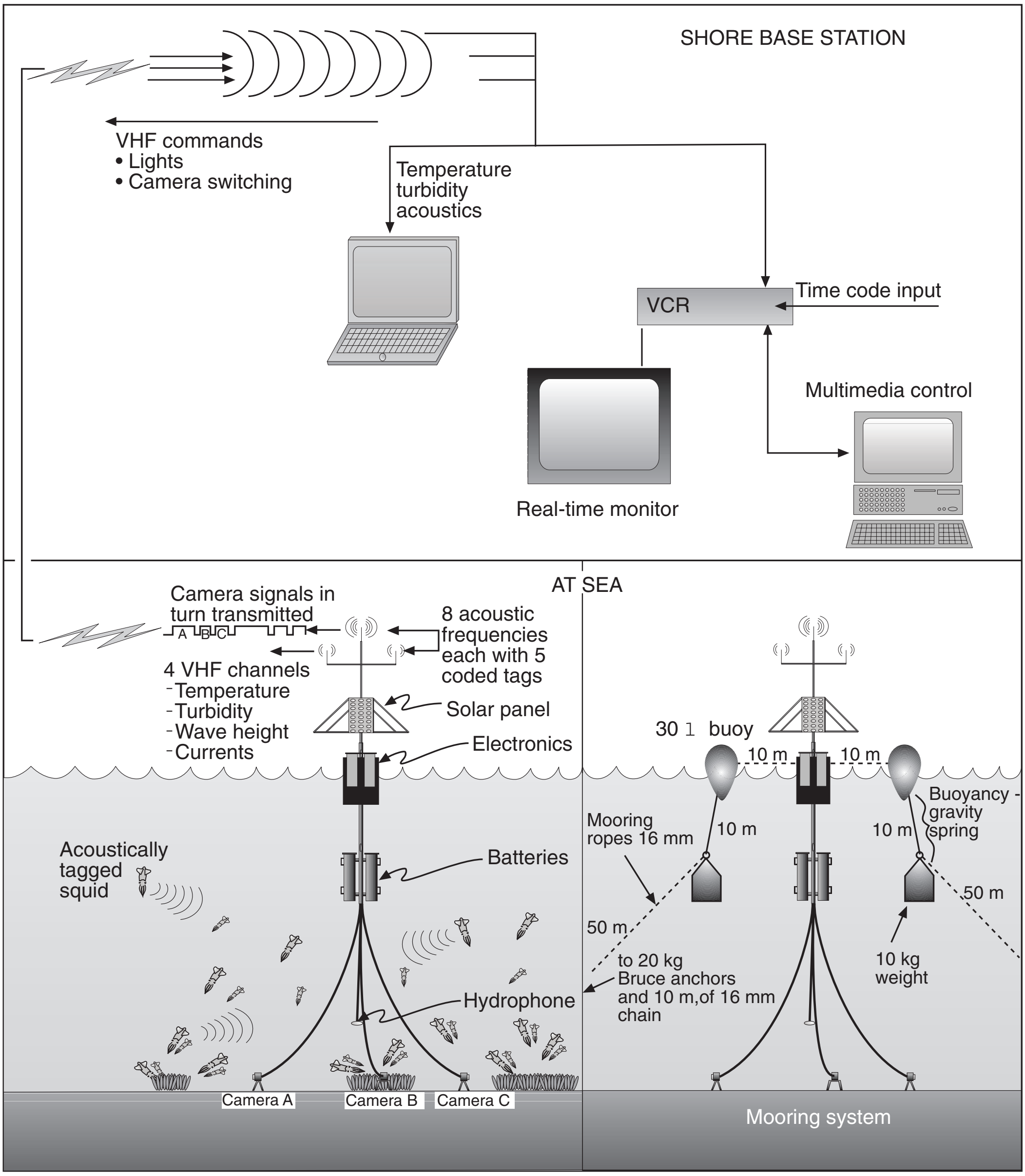

Fig. 9: Schematic diagram showing the main components of the hardware designed and constructed to quantify squid spawning behaviour and environmental influences

and abrasion.

The surface buoy may be positioned over the squid egg bed(s) using a two- (optional three-) anchor mooring system to maintain it in position while minimizing interference with the spawning process. Sufficient movement of the buoy is ensured by a "buoyancy-gravity spring" inserted in each mooring line (Fig. 9). This system also prevents rotation of the buoy and entanglement of the subsurface cables. Subsurface electrical cables are 60 m long, allowing monitoring over a sea-floor radius of 30–40 m, depending on water depth.

Several underwater video cameras (depending on the need) are mounted on sea-floor frames which can be positioned around egg beds by SCUBA divers. Underwater lights are mounted on the camera frames, which can be switched on at the shore station when necessary. Temperature, turbidity and wave height are measured on the sea floor. Data are transmitted to the surface buoy via the cables, where they are first stored onboard then telemetered to the shore station. To monitor the immigration and emigration of squid to and from the spawning aggregation, as well as to provide data during dark or turbid conditions, selected squid may be tagged with hydro-acoustic microtransmitters (supplied by VEMCO). The suspended mid-water hydrophone beneath the buoy can monitor up to 40 squid individually. This hydro-acoustic equipment allows for the distance of transmitters from the buoy to be determined and records the presence/absence of tagged squid within a determined radius of the buoy.

CONCLUDING REMARKS

In this paper, a working quantitative model to describe *Loligo vulgaris reynaudii* spawning aggregations and interactions with the environment has not been produced, but several important prerequisite steps towards this aim have been taken. The conceptual model, methodology and hardware developed here will permit *in situ*, quantitative, behavioural, physiological and environmental data to be collected. This dataset, however, will not be complete and reach its maximum potential without O_S and O_R data being collected simultaneously. Investigation of methods for collecting these data needs attention. Once this has been achieved, the remaining step to realizing the envisioned model is to select an appropriate model type (platform) which will best describe the processes and interactions, and ultimately the catches. Only then can such a model be coupled (or nested) with environmental models and used for forecasting purposes.

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APPENDIX

SPECIFICATIONS

CAMERAS

460-line, fixed focus, monochrome, RSL 12V DC

SHF VIDEO

Buoy	Transmitter buoy video frequency:	1 265 GHz
	Frequency control:	PLL
	Output power:	1.5W
	Modulation:	FM 15MHz deviation
	Pre emphasis:	CCI R405
	Video input:	1V P-P 75 Ohm
	Audio:	FM 6MHz subcarrier
	Audio response:	150 MHz – 5 kHz
	Power consumption:	1A @ 12V
Receiver base station		
	Sensitivity:	100 dBm
	Demodulation:	PLL with CCIR 405
	Video output:	1V P-P
	Audio output:	100 mV

HF TELEMETRY

Receiver base station		
	Transmitter base:	141.850 MHz
	Power output:	5W
	Modulation:	FSK (FM) 4 switched channels using audio tones
	Antenna:	50 Ohm
Buoy		
	Frequency:	141.850 MHz
	Sensitivity:	0.3V 12dB S-N
	Output:	4 switched channels (4A each) using PLL decoder
	Consumption:	12V (standby)

BATTERIES

6 × lead acid 12V DC 65 A/H connected in parallel with a voltage regulator

SOLAR PANELS

3 × 75W Siemens