1984

The Reproductive Behaviour And Ecology Of Smallmouth Bass (micropterus Dolomieui) In Long Point Bay, Lake Erie

Gregory Peter Goff

Recommended Citation

Goff, Gregory Peter, "The Reproductive Behaviour And Ecology Of Smallmouth Bass (micropterus Dolomieui) In Long Point Bay, Lake Erie" (1984). *Digitized Theses*. 1390.
https://ir.lib.uwo.ca/digitizedtheses/1390

CANADIAN THESES ON MICROFICHE

I.S.B.N.

THESES CANADIENNES SUR MICROFICHE

National Library of Canada
Collections Development Branch

Canadian Theses on
Microfiche Service

Ottawa, Canada
K1A 0N4

Bibliothèque nationale du Canada
Direction du développement des collections

Service des thèses canadiennes
sur microfiche

NOTICE

The quality of this microfiche is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us a poor photocopy.

Previously copyrighted materials (journal articles, published tests, etc.) are not filmed.

Reproduction in full or in part of this film is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30. Please read the authorization forms which accompany this thesis.

THIS DISSERTATION
HAS BEEN MICROFILMED
EXACTLY AS RECEIVED

AVIS

La qualité de cette microfiche dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de mauvaise qualité.

Les documents qui font déjà l'objet d'un droit d'auteur (articles de revue, examens publiés, etc.) ne sont pas microfilmés.

La reproduction, même partielle, de ce microfilm est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30. Veuillez prendre connaissance des formules d'autorisation qui accompagnent cette thèse.

LA THÈSE A ÉTÉ
MICROFILMÉE TELLE QUE
NOUS L'AVONS REÇUE

Canadä

THE REPRODUCTIVE BEHAVIOUR AND ECOLOGY OF SMALLMOUTH BASS (MICROPTERUS DOLOMIEUI) IN LONG POINT BAY, LAKE ERIE

by

Gregory P. Goff

Department of Zoology

Submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy

Faculty of Graduate Studies
The University of Western Ontario
London, Ontario
June, 1984

ABSTRACT

The reproductive behaviour and ecology of the smallmouth bass, Micropterus dolomieui, was studied during the 1981 to 1983 spawning seasons at Long Point Bay, Lake Erie. SCUBA was used to find and observe nesting males. My observations of these fish revealed some behaviours that were not previously described. Other activities, i.e. parental guarding, were segregated into discrete behaviour patterns. These units were organized into an ethogram of reproductive behaviour. A mating system involving selectivity by males in choosing mates was discussed.

Reproductive success of individual male smallmouth was measured by collecting new "black-fry" from nests. Thirteen variables reflecting differences in biological characteristics of the male, time in the season and particular habitat features in or near the nest were measured. The significant influences on reproductive success were evaluated through a sequence of statistical analyses. Principal components analysis on the 13 predictor variables provided a subset of 5 independent component variables containing 95% of the original variation. A multivariate analysis of variance on the PC scores of the variables indicated differences between years. Discriminant function analysis using data from different years as groups, identified that the physical environmental component (primarily the accumulated hours of wind greater than Beaufort force 4 during offspring development) was responsible for these differences. Multiple regressions of the component variables with reproductive success demonstrated that windy hours and the material in the bottom of the nests significantly influenced the numbers of "black-fry" in nests.

Renesting by male smallmouth that prematurely lost their brood was studied using 54 marked fish. Nest mortality was simulated by removing "black-fry". Twelve males (22%) undertook a second reproductive effort in their same territory. Renesting males were older and larger than those males that nested only once in a territory. Numbers of "black-fry" on both efforts did not differ significantly. All renesting males reared offspring to the "black-fry" stage a second time. Renesting effectively mitigated the failure of a first reproductive effort in one season.

ACKNOWLEDGMENTS

I take great pleasure in acknowledging the people who, to greater or lesser extents, have contributed to this thesis in various ways. Current and former graduate colleagues and my advisory committee all helped to focus my ideas. The criticisms of Dr. Dave Ankney and Keith Somers were particularly valuable as was the competent field assistance of Rob Rupert. The frequent and often lengthy discussions with my office-mate Helene Dupuis were beneficial, irrespective of the topic.

The knowledge, support and availability of my supervisor, Dr. Miles Keenleyside, made my residency in his laboratory stimulating and rewarding. The friendship of both Miles and his wife Hilda was greatly appreciated.

Extra-special recognition and gratitude go to the extra-special people who participated in the successful completion of this thesis. My wife Gillian undertook four years of hard work and challenge with good humour and unwavering support. Our children Danielle, Alicia, Peter and Meaghan gave new meaning to the words 'resilience' and 'good nature', especially during the busy periods of research and thesis preparation.

An N.S.E.R.C. operating grant to M.H.A. Keenleyside supported this research. Jim Collins with the Ontario Ministry of Natural Resources at Simcoe assisted with the logistics by providing boat and shore facilities. G.S. Goff typed the manuscript. A. Vincent drafted the figures.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

CHAPTER 1 - INTRODUCTION

Behaviour has evolved as a means of solving problems. To survive and reproduce an animal must solve a set of ecological problems and a set of social problems. The ecological problems involve finding a place to live and reproduce, acquiring resources and avoiding predation. Social problems include finding mates and rearing young (Wittenberger 1981: 195).

Some details of these problems of survival were examined in a study of the reproductive biology of smallmouth bass, _Micropterus dolomieui_. Specifically the reproductive behaviour and the reproductive success of male smallmouth nesting in a large shallow lake were observed and measured.

The smallmouth is one of the black bass or Micropterinae members of the sunfish (Centrarchidae) family (Hubbs and Bailey 1938). It is a warm water fish originally occurring in fresh waters of eastern central North America (Scott and Crossman 1973). However it has been introduced widely throughout North America and to Europe and Africa as a popular gamefish (Robbins and MacCrimmon 1974).

Centrarchid fishes in general have been the centre of much recent research on reproductive biology. Bain and Helfrich (1983) examined the relationship between offspring survival and nesting behaviour of _Lepomis macrochirus_. Bietz (1980, 1981) studied nest aggregation patterns in _L. megalotis_ and Dominey (1981a, 1981b) described female mimicry and the anti-predator function of nesting colonies in _L. macrochirus_. Gross (1982, 1983) and Gross and Charnov (1980) analyzed reproductive strategies and alternative life histories in _L. macrochirus_ and _L. gibbosus_. Gross and Nowell (1980) and Noltie

(1982) studied the reproductive biology of *Ambloplites rupestris*. Keenleyside (1972, 1978) studied fertilization stealing in *L. megalotis* and reproductive isolation between *L. megalotis* and *L. gibbosus*.

More specifically, *M. dolomieui* has been studied only minimally in the context of renewed interest in reproductive biology. Winemiller and Taylor (1982) and Schneider (1971) reported briefly on field observations of the nesting behaviour of smallmouth bass. A broader base of information came from more general studies on the biology of smallmouth. Reighard (1905), Beeman (1924) and James (1930) were the original sources of behavioural observations on spawning. Tester (1930) and Neves (1975) contained incidental behavioural information. A monograph by Hubbs and Bailey (1938) and review articles by Coble (1975) and Miller (1975) synthesized the literature on habitat requirements, growth and social behaviour (including reproduction).

One important aspect of reproductive behaviour is the degree to which it is successful. Our current measure of reproductive behaviour in meeting some of the ecological and social problems of a species is fitness. This central concept of evolutionary biology includes 'individual fitness' which measures the reproductive success of phenotypes (Wittenberger 1981: 47), and 'inclusive fitness' which accounts for gene representation in both immediate offspring and through relatives (Hamilton 1964).

Reproductive success is often used as an operational estimator of fitness. It has been measured in various ways across a range of fish taxa. Bain and Helfrich (1983) measured larval bluegill survival and Fitzgerald and Keenleyside (1978) used the percentage of surviving *Cichlasoma nigrofasciatum* progeny as reproductive success. Grant and

Colgan (1983) counted Etheostoma nigrum eggs in a male's territory while Kodrick-Brown (1983) used the number of females mated by each territorial male Cyprinodon pecosensis to indicate reproductive success. Perrone (1978) counted egg clutch size in Cichlasoma maculicauda and Schmale (1981) used the number of egg batches obtained per week in Eupomacentrus partitus to estimate reproductive success. In these studies reproductive success was evaluated against various conditions of behaviour (male parental care or courtship behaviour), morphological variation (male size and coloration) and environmental variation (substrate composition, topographic complexity and population density).

The purpose of the present study was to contribute further evidence to the accumulation of comparative knowledge on the reproductive biology of centrarchid fishes. Research on the reproductive behaviour and ecology of smallmouth bass was chosen as the means of meeting this objective. Two approaches were initially selected. First, observations were made of the nesting behaviours of male smallmouth in a natural, uncontrolled environment. These observations were used to evaluate the accuracy and completeness of the available descriptions of nesting behaviour of smallmouth, most of which originated from bass in culture ponds and aquaria.

Secondly, data were collected on the reproductive success of nesting males. Smallmouth bass were considered highly suitable for measuring reproductive output among individuals. A distinctive "black-fry" stage in the offspring development provided a reliable point at which to quantify reproductive success at the nest. This measure was analyzed in relation to characteristics of the nesting male and physical properties of the nest environment. The null hypothesis predicted that in a large, shallow, productive lake these influences did not have a significant effect on the reproductive success of nesting male smallmouth. Any significant influences on reproductive success discovered were discussed.

CHAPTER 2 - BACKGROUND

2.1 The Bay

Long Point Bay is a large shallow bay created near the eastern end of Lake Erie by a 41 km sand spit extending southeast from the north shore (Figure 2.1). A smaller second sand spit lying in a north-south direction creates an Inner Bay and Outer Bay.

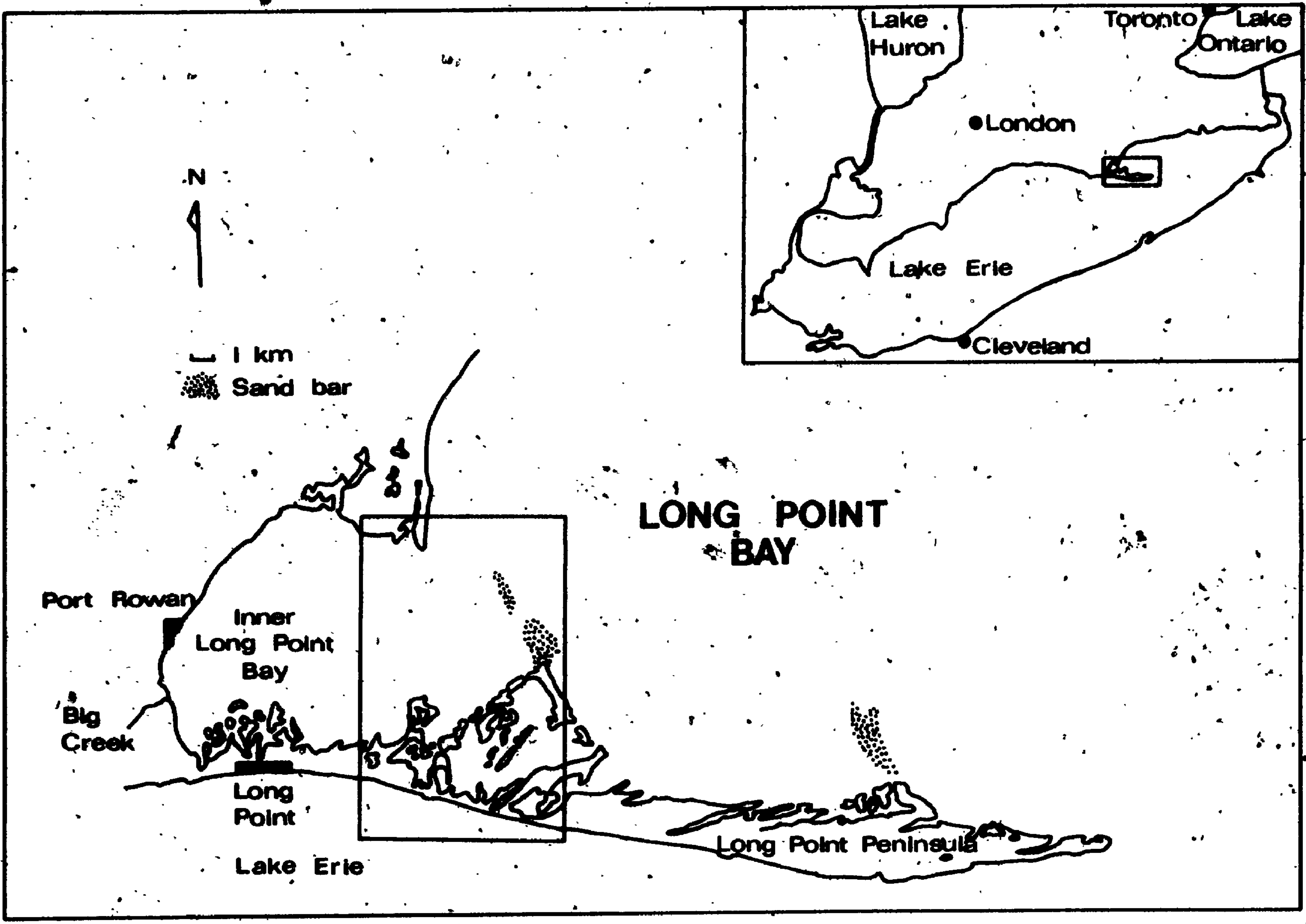
The Inner Bay covers 7,300 hectares, has a maximum depth of 3.05 m and a shoreline length of 40.7 km. Big Creek, its main tributary, has a mean daily discharge approaching 1% of the volume of the Inner Bay (Leach 1981).

The entire area is underlain by thick Palezoic sedimentary rock. The bottom of the bay is sandy mud, the nearshore areas being sandiest and the offshore areas progressively muddier. Nearshore sediments in the Outer and Inner Bays are about equal parts of sand, silt and clay (Heathcote 1981). Prevailing winds over Long Point Bay average 10 km/hr and are from the south and west (Kohli and Farooqui 1980).

The limnology of the Inner Bay was studied by Berst and McCrimmon (1966) and Leach (1981). The high coverage of the bottom of the bay by aquatic vegetation (approximately 90%) was described in both studies. The inner bay was classed as eutrophic and the outer bay was mesotrophic based on total phosphorus concentration and chlorophyll 'a' standing crops (Leach 1981). Smith (1979) identified Chara vulgaris and Myriophyllum spicatum as the predominant species in sandy and sandy loam sediments. Vallisneria americana and Najas flexilis and Potamogeton friessii were other common aquatic macrophytes.

The fertile Inner Bay supports vigorous recreational fisheries

Figure 2.1 Outline of Long Point Bay with study area indicated by rectangle in larger map (see Fig. 2.3). Insert map in the upper right corner marks the location of Long Point Peninsula within the Great Lakes.


Lake Huron
Toronto
Lake Ontario
London
Lake Erie
Cleveland
N
1 km
Sand bar
LONG POINT BAY
Port Rowan
Inner Long Point Bay
Big Creek
Long Point
Lake Erie
Long Point Peninsula

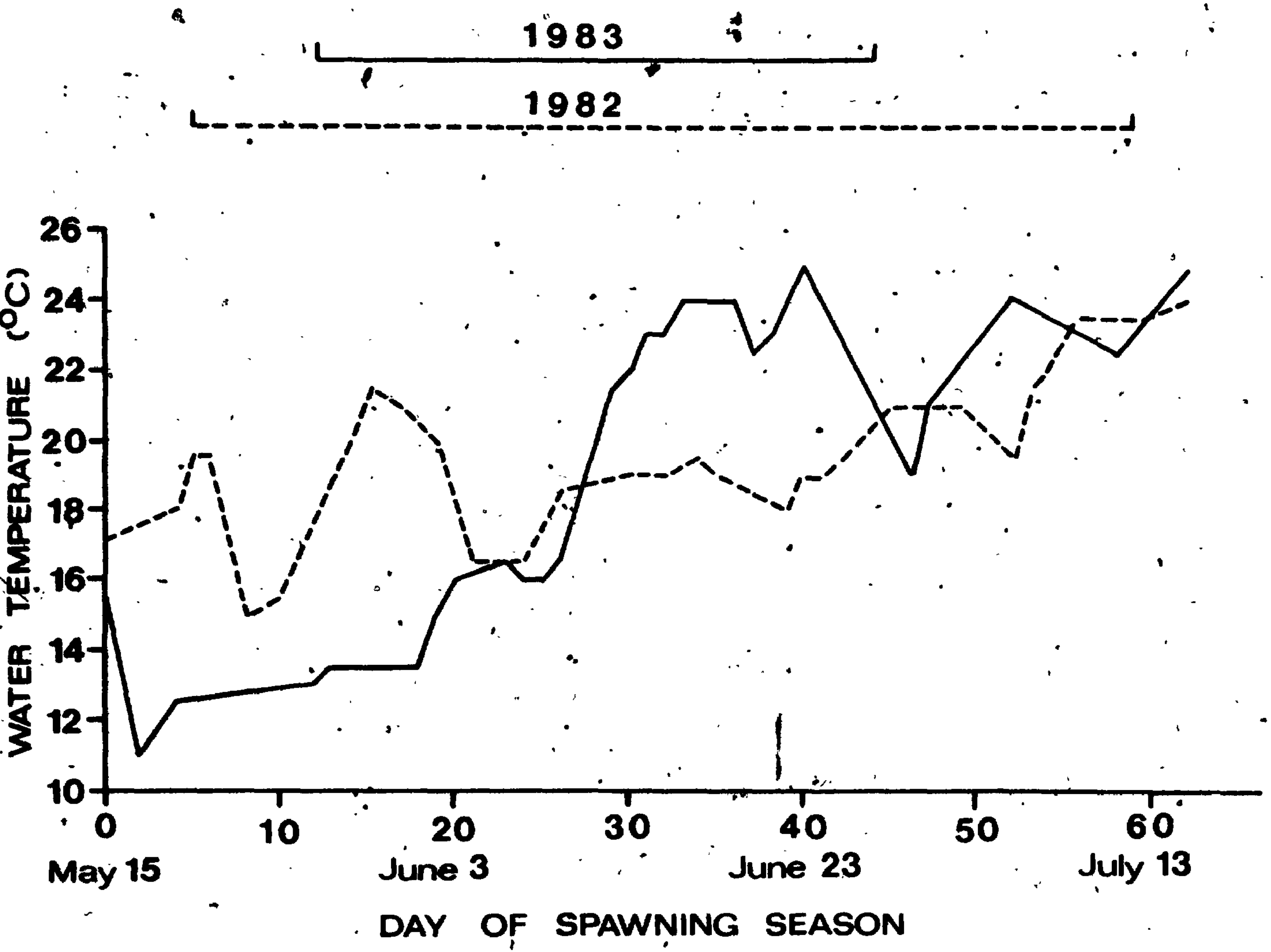
for yellow perch (Perca flavescens), rock bass (A. rupestris) and smallmouth bass (M. dolomieui). Annual creel censuses from 1979 to 1983 indicate recreational smallmouth catches ranging between 56139 and 73461 fish. The catch per unit of effort (CUE) for smallmouth anglers over the period ranges from .21 to .29 fish per hour of angling (Table 2.1). Sport hunting, wildlife observation, boating and swimming are other popular water based activities on the Bay.

The water quality of the Bay is the best in nearshore Lake Erie (Heathcote 1981) and its shallow waters provide excellent habitat for fish spawning. The Inner Bay warms rapidly in the spring, attains high temperatures in the summer and cools quickly in the autumn. The water temperature regime for the 1982 and 1983 spawning periods are in Figure 2.2.

Table 2.1 Annual recreational harvest of smallmouth bass from Long Point Bay between 1979 and 1983. The smallmouth catch per hour of effort (CUE) is based on angling for all species. (Data courtesy of Ontario Ministry of Natural Resources, Simcoe.)

Year	Number of Smallmouth Harvested	CUE Smallmouth Bass
1979	71,646	.225
1980	46,306	.209
1981	56,139	.206
1982	73,461	.281
1983	66,712	.290

Figure 2.2 Water temperature curves for Inner Long Point Bay during the 1982 and 1983 field seasons. The duration of nesting activity is indicated by the bars above the curves.


1983
1982
WATER TEMPERATURE (°C)
26
24
22
20
18
16
14
12
10
0
10
20
30
40
50
60
May 15
June 3
June 23
July 13
DAY OF SPAWNING SEASON

2.2 The study sites

The southern shoreline of the Inner Bay was historically considered a traditional smallmouth spawning area (Reid 1981). The field research was conducted along a 6 km stretch of shoreline within this area known as Little Rice and Big Rice Bays. Six study sites were chosen. These were spaced at approximately 1 km intervals (Figure 2.3). Each site was limited to the region (i.e. 100 m radius) around each chosen spot. Specific nests were located by random underwater searches, using SCUBA, in the restricted area of each site. All sites were repetitively and thoroughly searched to assure a high probability of sampling all nesting males.

Figure 2.3 Location of the study sites within Inner Long Point Bay (●). The water temperature station is indicated by ⊠ .

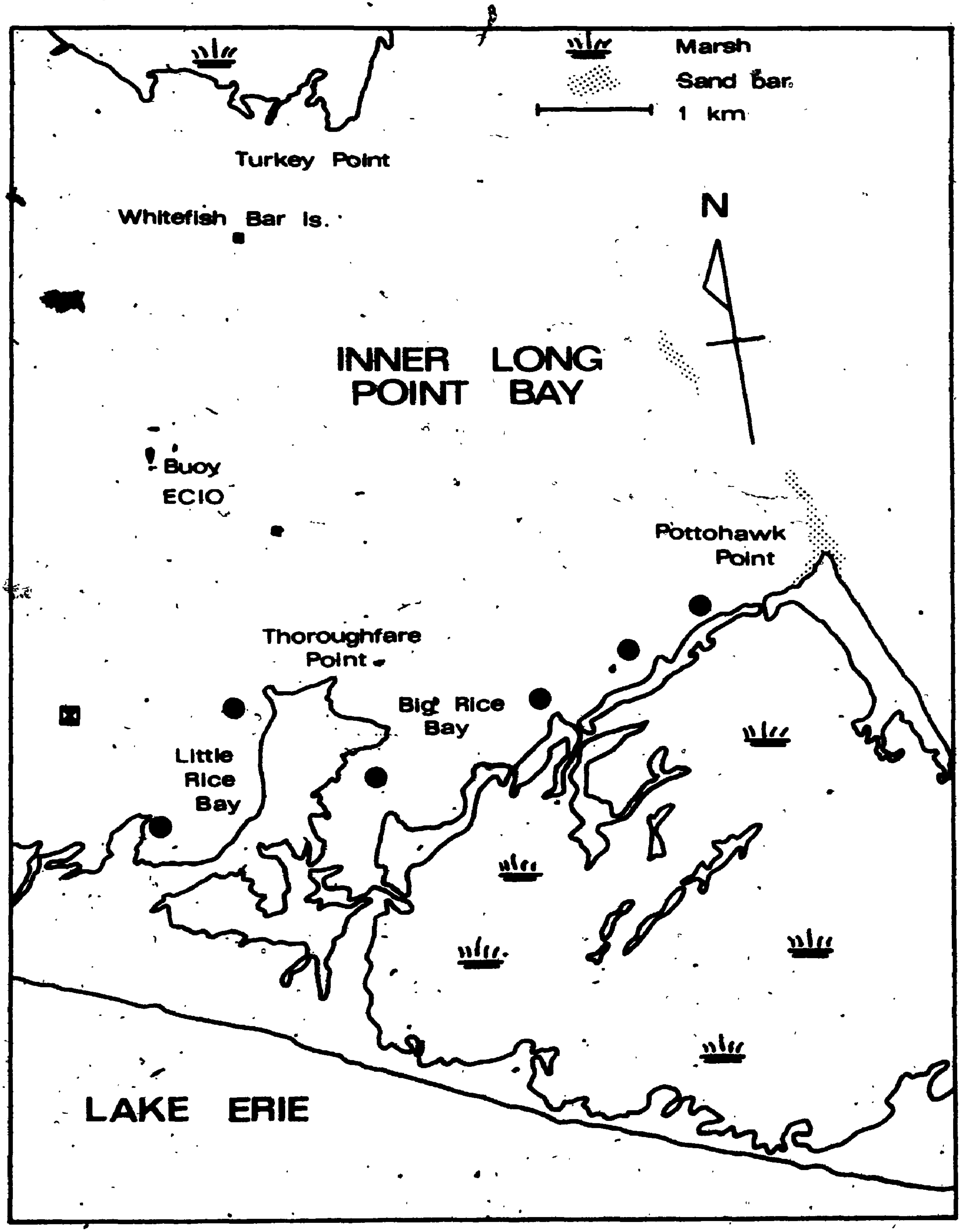
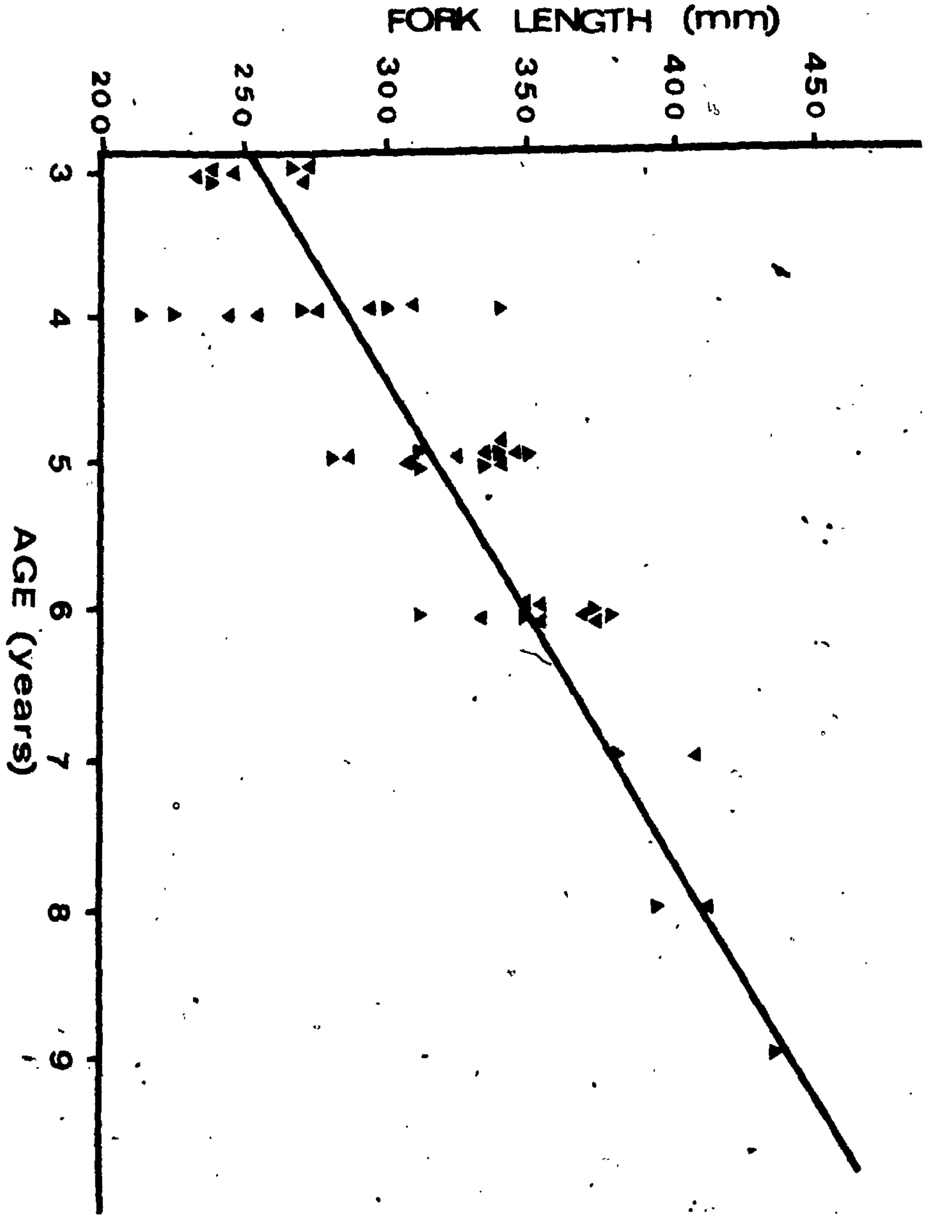

Marsh
Sand bar
1 km
Turkey Point
Whitefish Bar Is.
N
INNER LONG POINT BAY
Buoy ECIO
Pottohawk Point
Thoroughfare Point
Big Rice Bay
Little Rice Bay
LAKE ERIE

Figure 2.4 The size at age regression of successful male smallmouth bass in Long Point Bay was Fork length = 161 + 30.9 (Age), (r^2 = 80%).


FORK LENGTH (mm)
200
250
300
350
400
450
AGE (years)
3
4
5
6
7
8
9

2.3 General biology

Research on fish in Long Point Bay is minimal. Published literature includes: Goff (1984a, b) on reproductive biology of smallmouth bass, Whillans (1979) on fish community transformations, MacLean and Teleki (1977) on homing in rock bass, Sztramko and Teleki's (1977) study of fecundity variations in yellow perch, and Kelso and Frank's (1974) survey of organochlorine and heavy metal residues in yellow perch, white bass (Morone chrysops) and smallmouth bass. Reid's (1981) spawning survey and other Ontario Ministry of Natural Resources information, i.e. annual creel census, provide limited information on smallmouth bass in Long Point Bay.

A brief synopsis of general information is presented to characterize the population I studied in Long Point Bay. The size at age relationship of male smallmouth was based on 1982 and 1983 spawners (Figure 2.4). Ages of nesting bass ranged from 3 to 9 years. Most of the males belonged to the 1977 and 1978 year classes.

These fish differ in spawning habitat and nest construction from the standard smallmouth model in reported literature. Generally nests are constructed of gravel, rubble, coarse sand, bedrock or a combination of two or more of these materials (Adams and Hankinsen 1928; Beeman 1924; Hubbs and Bailey 1938; Coble 1975). Long Point Bay smallmouth nested on fine grain sediments having mean particle diameters from 0.003 mm (silt) to 0.02 mm (fine sand). They either constructed a nest or simply selected a natural depression. Alternatively, short stems (4-7 cm) of Chara vulgaris were frequently used as a nest substrate. The average nest diameter (26.3 ± 12.2 cm) in Long Point Bay was substantially smaller than the published diameter of 60-120 cm (Hubbs and Bailey 1938).

The smallmouth moved into Inner Long Point Bay with warming water temperatures in the spring and emmigrated from the area when nesting was completed.

CHAPTER 3 - REPRODUCTIVE BEHAVIOUR

3.1 Introduction

Adaptive solutions to the basic survival and reproductive problems of all fish are most likely to be correctly perceived by workers who are familiar with the natural ecological setting of their animals (Keenleyside 1979). Because surroundings can distort and modify behaviour, a study should be made under conditions which are as natural as possible. Ideally this is in the wild state (Marler 1975).

The primary descriptions of reproductive behaviour of smallmouth bass are provided by Reighard (1905) and Beeman (1924) based on observations in hatchery ponds and James (1930) from aquarium observations. Reviews of reproductive behaviour which address smallmouth are found in Breder (1936), Hubbs and Bailey (1938), Breder and Rosen (1966), Coble (1975) and Miller (1975). Limited behavioural observations on natural populations are added by Cleary (1956), Pflieger (1966), Schneider (1971), Neves (1975) and Winemiller and Taylor (1982). However a comprehensive description of the characteristic behaviour patterns or 'ethogram' (Brown 1975) for smallmouth still awaits completion.

Observations were accumulated underwater on wild smallmouth bass in Long Point Bay. The research entailed two specific objectives. The first was to inventory and clearly describe all behavioural acts that occur during reproduction. The second was to organize these acts into groupings of some apparent functional similarity (Myrberg 1972, Lehner 1979).

3.2 Methods

Behavioural observations on nesting males were collected between May and July from 1981 to 1983 (Table 3.1). The study sites were visited regularly during each season and underwater searches were conducted. Two divers swam parallel holding the ends of a rope spacing them up to 2 m apart. The area covered on one search depended on the water visibility, which generally ranged from 0.5 m to 2.0 m. Thus, searches covered approximately 600 to 1600 m^2 of bottom during a swim of 200 m.

Active nests were marked by a numbered fluorescent surface float anchored to the substrate near the nest. These were revisited periodically. Fifteen minute behavioural observations were made on various males at different times through the reproductive cycle. Information was collected by a diver lying motionless on the substrate 0.5 to 1.0 m from the nest. Notes were recorded underwater on a scored plastic slate.

The common initial response of a guarding male towards an approaching diver was to move forward and display with all fins extended. This response habituated quickly and during periods of data collection the diver was ignored by the male smallmouth.

Table 3.1 Periods of sampling smallmouth reproductive behaviour from 1981 to 1983.

	Spawning Season		Behavioural Observations	
Year	Initiation	Termination	No. of Nests	Hours
1981	June 1	July 8	38	15
1982	May 19	July 12	28	10
1983	May 26	June 27	32	10
		Totals	98	35

3.3 Results

The general pattern of reproductive activities I observed corresponded to the descriptions of Reighard (1905), Beeman (1924) and Hubbs and Bailey (1938). Some behaviours I observed in the field were not reported by these authors. The behaviour patterns most frequently observed were described. These behaviour patterns were then organized into three general categories: territorial, spawning and parental care. The categories and a hypothesized function for each behaviour pattern are listed in Table 3.2.

3.3.1 Description of reproductive behaviours

Initiating: the male swims near a lightly scraped patch on the substrate. He swims continuously and may leave the scrape area for several minutes. The fish is not very aggressive, frequently ignoring nearby fish and is wary of divers. The spiny dorsal fin is folded and neither the black patch near the tip of the operculum (Scott and Crossman 1973) nor any markings on the lateral body wall are visible.

Alert display: the territorial male slowly moves a short distance off the nest to face a nearby fish or diver. The spiny dorsal fin is erect and the pelvic fins are extended clearly showing the white margins. The white spot at the tip of the operculum is distinctly highlighted against the black patch on the operculum. Four lateral facial stripes are visible and the vertical bars on the lateral body wall are faded. The display persists until the intruding fish departs or it habituates following a short exposure (i.e. 30 seconds) to a

Table 3.2 Reproductive behaviours in smallmouth bass.

Category	Behaviour Pattern	Hypothesized Function
Territorial	Initiating	- to establish a territory
	Alert display	- to threaten a territorial intruder
	Charge	- to aggressively remove an intruder
Spawning	Leading	- to attract a female to a territory
	Circling	- to direct a female into a nest
	Nipping	- to direct a female and stimulate spawning readiness
	Crossover	- to synchronize gamete release
	Quiver	- to mobilize eggs in ovary
	Inter-quiver pause	- to assure female of male readiness to actually release sperm - to increase female stimulation by male
	Spawning	- actual release of gametes
Parental Care	Fanning	- to remove silt by moving water over eggs
	Tilting	- to inspect nest contents
	Patrolling	- to maximize warning of intruders while guarding larvae
	Tail beat	- to threaten a larger intruder
	Defending	- to actively protect "black-fry" by aggressively removing predators.

motionless diver. An abridged form of this behaviour is occasionally displayed by a male while remaining over its nest.

Charge: a rapid approach towards another fish by a territorial male, initiated with a sudden burst of swimming. The spiny dorsal fin is raised, the white opercular spot and black highlight are clear and the vertical bars on the lateral body wall become darker and distinct. The charge generally terminates with the retreat of the intruding fish but occasionally the smallmouth butts the intruder with its mouth. The male always returns to the centre of its nest.

Leading: a slow non-aggressive swim towards a conspecific where the male is propelled by slow wide-amplitude beats of caudal peduncle and fin. The presence of female smallmouth nearby is frequently established when this behaviour is displayed.

Circling: male and female smallmouth swim in circles above the nest with the male on the outside. The circles decrease in diameter as the pair descends in the water column towards the nest. The male directs the female with butts or nips to her operculum. The female circles with her head inclined downwards.

Nipping: the male smallmouth occasionally bites the female near her operculum during the early stages of courting. This behaviour becomes more frequent and vigorous as the pair approach spawning and is directed towards the female's vent area.

Crossover: the pair settles in the nest with the posterior half of the female's body crossed over that of the male, creating an angle between 20 and 80 degrees between them. This may persist up to 30 seconds during the early stages of spawning. The male then aligns himself parallel with the female and she begins to quiver.

Quiver: the female rolls laterally 45 to 90 degrees so that her pectoral fin touches the substrate and her vent faces the male. She then quivers vigorously along her long axis for several seconds (2-5 seconds).

Inter-quiver pause: following several initial bouts of quivering the female rises 0.25 to 0.5 m above the substrate and circles the nest. The male nips vigorously around the female's vent until she returns to the crossover position.

Spawning: egg release occurs during a bout of quivering. However, during the initial and final bouts of quivers no eggs are shed. A red papilla through which the eggs are released extrudes from the female. Milt from spawning males is not visible. During intense spawning the inter-quiver pause is absent as the female rises only slightly off the bottom of the nest, turns and settles into the nest again.

Fanning: the male is positioned parallel to the substrate, 2-4 cm above the eggs. Spiny dorsal and pelvic fins are folded. Pectorals beat alternatively. Anal and soft dorsal fins work in opposition to the caudal fin. The male frequently changes orientation while positioned over eggs. He will interrupt fanning to display, or charge intruders.

Patrolling: the male swims in small diameter (0.5 to 1.0 m) circles and "figure 8 patterns" around the periphery of the nest, approximately 10 to 15 cm above the larvae on the substrate. This activity is occasionally interspersed with alert displays and charges. The male returns to the centre of the nest and resumes patrolling following these interruptions.

Tilting: the male interrupts fanning of eggs and moves slightly backwards using his pectoral fins. Then he inclines forward into the nest for several seconds. Fanning is resumed.

Tail beat: the fish swims against a large object (i.e. diver, dredge, spear handle) intruding into the nest territory. He rolls to make contact using the anterior dorso-lateral body wall. The fish runs its body wall along the object and terminates the motion with a strong beat of the caudal peduncle against the object. This produces an audible low frequency sound. The white opercular spot and the black highlight are present. Vertical bars are visible on the lateral body wall and facial stripes are visible. This behaviour likely functions as a warning or aggressive display to a large intruder.

Defending: the male swims around the periphery of a cloud of free swimming "black-fry" that have risen out of the nest. He is preoccupied with charging lurking predators (e.g. rock bass and pumpkinseed) when they attempt to take "black-fry" on the periphery of the cloud.

3.3.2 Organization of reproductive behaviour

Territorial behaviour

The earliest sign of a new nest was a spot or 'scrape' on a sand or clay substrate where the surface sediment was scraped away to reveal a dark patch. The male was non-aggressive and wary of divers. It often took the fish several minutes to habituate and return to the nest. Territoriality was confirmed by the fact that one male always returned to the same newly scraped area after each foray from the nest. Up to three adjacent scrapes were found at one site, however only one received eggs.

Where depressed Chara sp. was used as a nest substrate, the scrape was not always visible when a territorial male was encountered. In other instances eggs were spawned on short standing Chara sp. adjacent to a scrape.

Territorial establishment lasted from several hours to a couple of days during which the initial site fidelity of the male was reinforced as the male's aggression increased. The male exhibited alert displays or charged other fish at the nest. The alert display and charge were used by the male throughout all stages of the reproductive cycle. These behaviours excluded other fish during the establishment of a nesting territory and warded off other males that intruded too close to spawning activity. These same behaviours were used to protect hatched offspring from predators.

Spawning behaviour

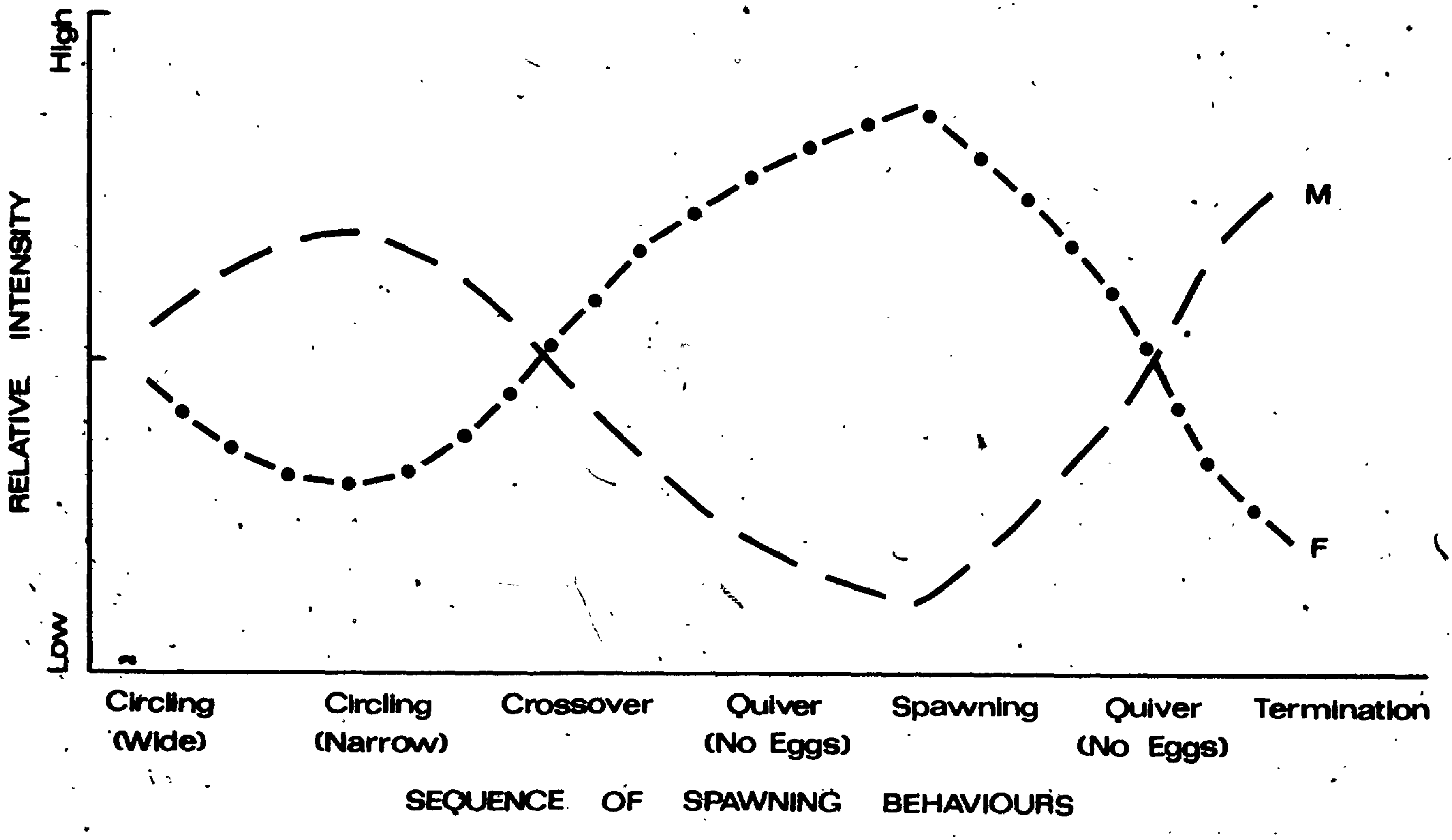
In contrast with the aggressive and rapid moving charge the slow leading swim was evidence of the readiness of the male bass to spawn. Females responded positively to this behaviour by remaining in or near the territory.

In 6 out of 7 complete spawning sequences observed, the female smallmouth was larger than the resident male. In the remaining pair both fish were of equal size. In all cases the male initiated circling behaviour in his territory by nipping the female on the operculum. Initially the pair swam horizontally in large diameter circles well above the nest (0.5 to 1.0 m). Females occasionally terminated courtship at this stage. As the courtship progressed the pair descended in the water column and eventually settled into the crossover position in the nest. The initial quivers when no eggs were released were interspersed with inter-quiver pauses during which nipping by the male became intense.

The early quivers were succeeded by a series of bouts of egg deposition, with approximately 30 seconds between bouts. The inter-quiver pause was eliminated as the female simply turned in the nest and resettled to release more eggs.

The decline of spawning was signalled by the resumption of the inter-quiver pause and an increase in nipping by the male. The female no longer shed eggs during bouts of quivering. Spawning terminated and the female left the territory, presumably facilitated by the resurgence

Figure 3.1 Changes in the relative intensity of male (M) aggressiveness (— —) and female (F) readiness to spawn (· — ·) during one spawning cycle. Labels on the horizontal axis indicate the order in which these behaviour patterns become prevalent.


High
Low
RELATIVE INTENSITY
M
F
Circling (Wide)
Circling (Narrow)
Crossover
Quiver (No Eggs)
Spawning
Quiver (No Eggs)
Termination
SEQUENCE OF SPAWNING BEHAVIOURS

in aggressive nipping by the male.

The interaction of male aggression and female readiness to spawn is summarized in diagramatic Figure 3.1. Following initial pairing the frequency of aggressive male nipping increased as he attempted to direct the female to swim in tighter circles and enter the nest. At that point a female sometimes departed and further courtship was terminated. However, if the female indicated her readiness to spawn by swimming in tighter circles and entered the nest, the intensity of male nipping decreased. Once the crossover stage was reached male aggression declined and all aggressive nipping was absent as spawning proceeded. When the female had spawned her eggs and additional quivers did not release eggs, the male's aggressive nipping resumed. It increased in intensity during the inter-quiver pauses at the nest until the female departed.

During the spawning sequence, a male occasionally suspended courtship to charge a nearby smallmouth but quickly resumed circling with the female. (A spawning pair seemed oblivious to a diver lying quietly near the nest.)

Males often spawned with two or more females. Evidence of multiple spawning was observed in nests containing eggs approximately 24 hours old (as indicated by their accumulation of settling sediment particles) and more recently spawned eggs. Occasionally a male with a clutch of eggs was seen leading, presumably in an attempt to entice another female to spawn.

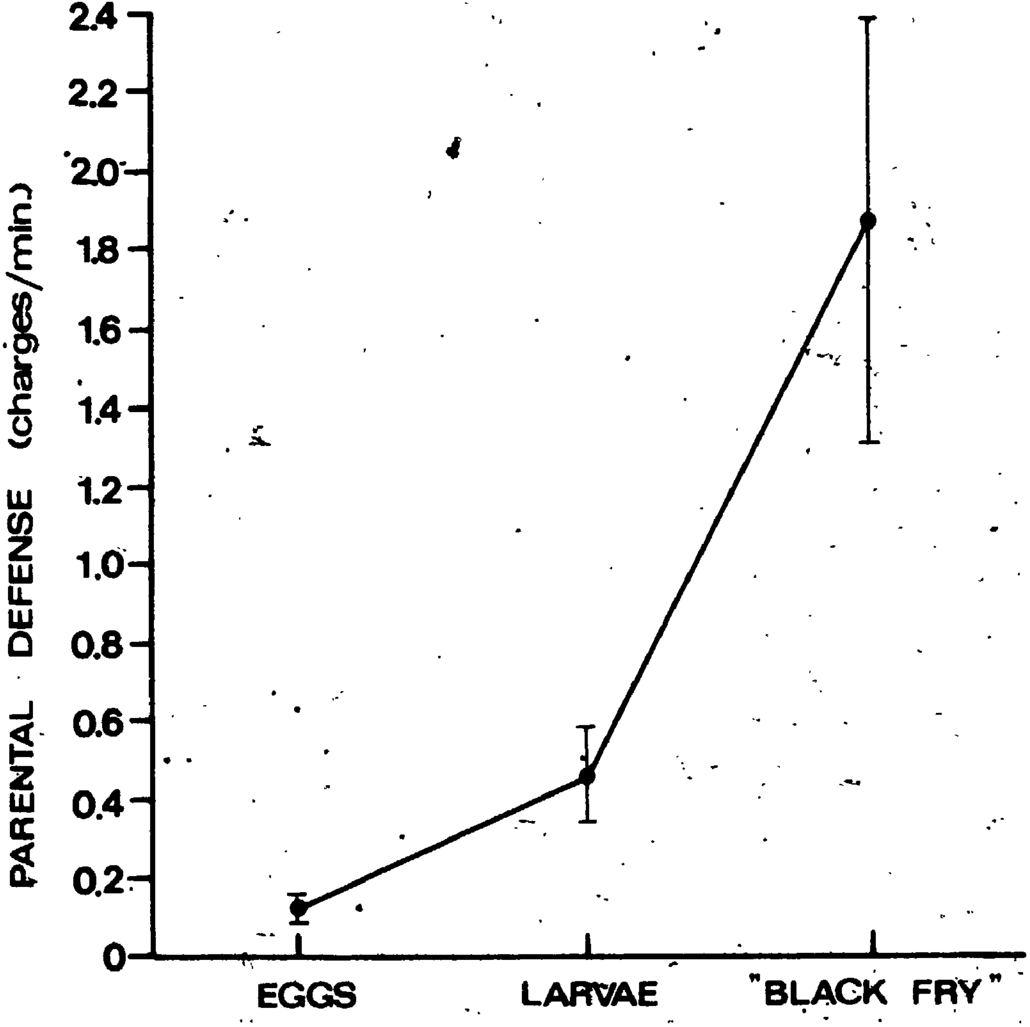
Parental care behaviour

Males with eggs spent most of their time fanning immediately above the nest. Swimming activity was restricted and alert displays and charges were minimal. The radius from the nest of swimming activity and frequency of alert displays and charges increased as the offspring developed into larvae and "black-fry". During patrolling the male swam the perimeter of its nest and the frequency of charges increased slightly. This activity increased dramatically while defending the "black-fry" (Figure 3,2).

The period when the male defended the cloud of swimming "black-fry" was the most demanding in terms of parental care. Rock bass (A. rupestris), pumpkinseed (L. gibbosus) and yellow perch (P. flavescens) were predators that continually prowled nearby. These fish successfully captured "black-fry" from the periphery of the cloud when the guarding male was absent or distracted. Consequently the male smallmouth was almost continually displaying warnings and charging. The rushes from one end of the cloud of "black-fry" to the other to drive off predators greatly increased the radius of the male's activity from the original nest.

Tilting and tail beats were observed during the parental care phase. Both behaviours occurred during the period of egg development. Tail beats were also seen when larvae were in the nests.

Figure 3.2 Changes in the frequency of charges by a male towards predators at different stages of offspring development. Charging frequency was recorded during 15 minute sampling periods. Vertical bars indicate ±1 standard error.


PARENTAL DEFENSE (charges/min.)
2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0
EGGS
LARVAE
"BLACK FRY"

3.4 Discussion

The existing description of reproductive behaviour in smallmouth bass was considered incomplete and imprecise for two reasons. First, there was a lack of description of appropriate discrete behavioural units as suggested by Altmann (1974). For example I refined the general ability of a nesting male to "chase away other smallmouth" (Reighard 1905; Hubbs and Bailey 1938) into reliable, descriptive behavioural units. The alert display and charge behaviours were consistent in form and effectively removed intruding smallmouth from a resident male's territory.

The selection of appropriate units of behavioural description greatly facilitates understanding an animal's behaviour. The combination of erect fins and specific body markings of the alert display is the initial signal of a territorial male to a nearby fish. When the alert display does not effect withdrawal of an intruder or predator, the more aggressive charge is performed. In rare instances the charge ends when the male smallmouth butts the unwelcome fish with its mouth. These refined descriptions also demonstrate the economy of behavioural organization. The least energetically expensive behaviour that commonly achieves the objective is used initially (e.g. the alert display generally wards off territorial intruders).

The second weakness in the available descriptions of smallmouth behaviour was caused by the failure to use current underwater methodology in a thorough study of reproductive behaviour. Schneider's (1971) underwater descriptions were based on observations of a single spawning pair. Allan and Romero's (1975) study of spawning and survival in the related largemouth bass (M. salmoides) indicated the effectiveness of the SCUBA approach.

Schneider (1971) described 'false spawning' periods before and following actual spawning. He interpreted this as individual variation in the spawning sequence. My observations indicated that bouts of quivering without egg release both before and after quivering with egg release were normal stages in the sequence of spawning behaviours. It potentially provided a mechanism whereby a female could interact with a typically aggressive male to evaluate the quality of both the fish and his nest, without being committed to waste gametes on an unsatisfactory mating.

This research revealed some new behaviours that were not in the literature. The crossover behaviour was observed in all spawning pairs in Long Point Bay. A. Emery (personal communication) also observed and filmed crossover behaviour in a population of smallmouth at Algonquin Park in northeastern Ontario. This behaviour was important in synchronizing the behaviours of the male and female bass and presumably assured maximum fertilization. Male aggression disappeared at this stage.

The tail beat was another previously undescribed behaviour. It clearly functioned as a threat or warning to a large intruder. I did not ascertain whether the prime mechanism of communication using this behaviour occurred through tactile contact (i.e. the force of the tail on the intruder) or through the low frequency sound produced during the tail beat.

Parental guarding was partitioned into fanning, patrolling and defending because each behaviour was different and appeared most appropriate for protecting the offspring the males were guarding at that time.

The spawning observations provided some insight on the mating system of smallmouth bass. The larger size of the female in most spawning pairs was notable. A system of female choice was initially suspected since females visit males' territories. It was expected that a female would mate with the largest possible male (Williams 1975; Perrone 1978). There were three plausible explanations for this apparent deviation from the expected pattern.

First, the heavy recreational fishery for smallmouth bass overlapped with the breeding season. Possibly the highly vulnerable territorial males were caught and these smaller nesters were simply the largest of the available males.

Another explanation considered the aggressive nature of the territorial males. The high densities of predatory fish in this Bay stimulated the "super-normal" aggressiveness of nesting males. The aggression that females encountered was sufficient to deter them from remaining with males larger than themselves. The reactions of smaller males were potentially less physically damaging.

The third alternative was that the male-female size relationships reflected some degree of male choice in selecting a mate. Since fecundity was directly related to size in fish (Loiselle 1982), spawning with a larger female meant potentially higher numbers of offspring.

Current theory (Baylis 1981) claimed that a male should accept eggs from any female because the cost of sperm was much less than the cost of eggs and the potential increase in fitness (offspring numbers) should not be refused. The evidence of male multiple spawning supported this argument. However, more important was Loiselle and Barlow's (1978) consideration that where selection favoured active paternal care a male can accept eggs for only a brief period in order to coordinate his care with the needs of the brood. The omnipresence of predators in Long Point Bay dictated the need to synchronize offspring development so as to ensure the maximum efficiency of paternal care at any stage. Consequently the male's opportunity to garner eggs was temporally restricted.

Thus the best male strategy was to mate first with a large female and obtain a relatively large clutch of eggs. If no additional females were available in the next 24 to 36 hours a male has at least maximized his one spawning opportunity and could proceed to subsequent stages of parental care. The spawning contribution of any smaller female within the appropriate time following the first large female represented a bonus in offspring numbers.

By contrast a male that first accepted a small female obtained a relatively small clutch. The absence of additional spawning, within the restricted period prior to the onset of other parental behaviours, resulted in relatively low offspring numbers for that breeding cycle.

The generally high level of predation on smallmouth nests in Long Point Bay was evident. Yellow perch (P. flavescens) completely destroyed several nests, each containing approximately 1500-2000 "black-fry", within 4 minutes of removal of the nesting males. I observed a hierarchy by which the more common fish in the bay were chased during the parental care period. Yellow perch were always chased from a smallmouth nest while rock bass (A. rupestris) were chased most of the time. Other smallmouth bass were occasionally chased. Presumably this hierarchy reflected a decreasing degree of hazard of these fish as predators.

I interpreted the increasing frequency of charges by the nesting male (Figure 3.2) as the offspring developed as a response to increased predator effort over time. This was due to the larger size of the offspring, which enhanced their profitability as prey items (Krebs 1978). The increased movement of "black-fry" above the nest also increased their visibility. After the juvenile schooling period the surviving fry moved closer to the surrounding vegetation and became less obvious.

My research required that no disruptions of the nesting male were caused by the SCUBA methods used. My observations indicated that divers moving slowly and working quietly near a nest did not significantly disturb the normal activities of a nesting male or scare away spawning females.

CHAPTER 4 - REPRODUCTIVE SUCCESS

4.1 Introduction

Sexual reproduction produces variable offspring from two individuals which assures the continued representation of their genes in a fluctuating environment (Williams 1975). The effectiveness of an individual's sexual reproduction is measured by its 'individual fitness' or how well it produces descendents in comparison with other individuals in the population. Reproductive success, as an operational estimator of fitness, is studied in a population of smallmouth bass nesting in Long Point Bay.

The conditions at any nest are determined by differences in biological characteristics of the breeding fish, time in the season and particular habitat features. Any combination of factors may influence smallmouth reproductive success. Several of these factors have been reported. Temperature (Bennett 1965; Christie and Regier 1973), substrate (Bennett and Childers 1957), pH and dissolved oxygen (Tester 1930), turbidity (Robbins and MacCrimmon 1974), cover (Vogele and Rainwater 1975) and current (Winemiller and Taylor 1982) are all implicated as influences on successful reproduction in smallmouth bass. The present research examines certain physical and biological factors in the environment of nesting smallmouth. These are used to explain some of the observed variation in reproductive success in the population.

Two points were important in this approach to studying reproductive success. First, the research was conducted on that subset of male smallmouth bass that successfully spawned and reared offspring to the "black-fry" stage. These fish were territorial, parental and accessible for research in comparison with unsuccessful males which left their nests before the young became "black-fry".

Secondly, reproductive success was an estimate of 'relative' reproductive success, measured at the nest while the male was still with his offspring. This distinction was important as reproductive success could also be measured in other ways, e.g. the number of fertilized eggs (Clady 1975; Neves 1975) or the number of fry that survived the first winter (Fry and Watt 1955). Both of these measures were technically difficult to obtain. However, the measure I used was taken at the end of the first critical stage of reproduction (Hjort 1926). Hjort stated that extrinsic influences during this stage may have a disproportionate effect on a fish's annual reproductive output. In fact Eipper (1975) considered early mortality in smallmouth as the major determinant of annual reproduction.

A major advantage in using "black-fry" to determine smallmouth reproductive success was that this distinctive stage provided a fixed reference point in a continuous sequence of development. At this point the male has been with the offspring between 4 and 10 days, depending on water temperature which determined the development rate of offspring. His ability to accumulate eggs and provide protection for them was tested during this period.

Several steps were required in evaluating reproductive success in smallmouth bass. The first involved selecting a set of predictor variables that reflected the conditions of the nesting environment in Long Point Bay. The ultimate objective of the analysis was to determine the relationship between reproductive success and the factors that influenced it. In order to assure valid results the relationships among the predictor variables were first explored. These analyses resolved several initial questions with the data including: which predictor variables contained most variation in the nesting environment; were the predictor variables independent; did the influences change over the years the data were sampled; and if there were annual differences in the data, how could they be explained?

4.2 Methods

During the 1981 season a set of variables was selected to study reproductive success and various field techniques were evaluated. These methods were used during the 1982 and 1983 field seasons to collect the data.

4.2.1 Field methods

The work was done from a 5.5 m boat, using SCUBA. The study sites were searched regularly and active nests were marked as described in Chapter 3. Marked nests were revisited periodically to determine their progress. Smallmouth offspring were collected within 24 hours of transforming from larvae to "black-fry". This stage was characterized by increased dark pigment in the young and their rise from the substrate to swim in the water column (Hubbs and Bailey 1938). A low pressure suction dredge (Appendix 2) run from a SCUBA tank was used to collect the "black-fry". These were preserved in 10% formalin and labelled.

In 1982 the nest-guarding males were collected when the "black-fry" were taken, using a hand spear or long handled fishing net, and were measured immediately in the boat. In 1983 the males were caught alive with a hand net and measured underwater with a metal ruler when the "black-fry" were collected. Scales were taken and the fish were individually marked with a unique combination of 3 and/or 6 mm diameter holes punched in their fins with single hole paper punches. These fish were then released. The normal behaviour and healing of the punctures in fish that renested indicated the method did not damage the fish.

Measurements of the nest were also taken when the offspring were collected. Underwater notes were recorded on a scored plastic slate.

General habitat measurements on sediment and vegetation were taken in each study site at two week intervals through both nesting seasons. Three 100 ml substrate samples were randomly sampled in a rigid cylinder (3.6 x 10 cm), bagged and taken to the lab. The modal vegetation height and portion of substrate covered by vegetation were measured and recorded on 25 random tosses of a 0.5 m square quadrat. The portion of covered substrate was recorded as an integer 0,1,2,3,4 representing the absence of vegetation or increments of approximately ¼ portions of the quadrat. The data were used to construct curves of seasonal changes in these variables.

Water temperature was recorded daily at mid-day at a fixed station. Temperatures were recorded 15 cm below the surface with a hand held mercury thermometer. Water temperature at the nests never varied more than 1.5°C from that at the fixed station. The temperatures at the fixed station were used as a standard for all spawning since these data were most complete. The depths of the nests below the water surface were measured on days when the water in Long Point Bay was at a constant level on a graduated water depth meter.

4.2.2 Laboratory methods

The preserved "black-fry" from each nest were rinsed and evenly distributed over a 1 mm mesh circular sieve (20 cm diameter) using flotation. A cardboard overlay with a 10% sector cut out was randomly dropped in the sieve to subsample the fry. These were removed, re-distributed on another sieve and counted. Five of these subsamples were taken from the original distribution and the total number of "black-fry" was calculated. This value represented the reproductive success of that nest.

Several scales were taken from two places on each male. One was immediately posterior to the point of the operculum and the other was on the dorsal body wall mid-way between the opercular point and the origin of the spiny dorsal fin. Impressions of 6-8 scales were made on acetate slides for each fish. Enlarged microprojector images of annular rings were counted to determine a fish's age (Bagenal and Tesch 1978). The technique was validated by comparing ages on duplicate scales aged by Ontario Ministry of Natural Resources personnel at Wheatley, Ontario. Ninety-one percent concurrence on the first reading was realized.

The sediment cores were oven-dried in enamel pans overnight and weighed. The density of the sediments in each study area was calculated and seasonal curves were drawn.

Wind records for Long Point were obtained from the Atmospheric Environment Service of Environment Canada. Anemograph chart records summarized to hourly wind force and direction were used. The hours of wind over the nest in excess of Beaufort force 4 (Kraus 1974) were totalled for each nest. This was done for the period of offspring residency. (Estimates of this residency period were based on regressi[illegible]s of known durations between spawning and "black-fry" collection for 21 and 41 nests in 1982 and 1983 respectively.)

4.2.3 The variables

The set of physical and biological variables used to study the reproductive success of smallmouth bass are briefly described in Table 4.1. Some additional detail is required. Date was an indication of the time during the spawning season when the nest was successful. May 15 was used as the first possible day of smallmouth spawning in Long Point Bay to assure that the field season predated the initial spawning activity. The selection of windy hours in excess of Beaufort force 4 was based on observations of mechanical disruption and dispersion of eggs and larvae in nests at these forces. Wind blowing from the direction of the closest shoreline was not associated with these effects. Consequently wind recorded from three open water quadrants (i.e. 270 degrees) provided the best measure of wind. These effects were observed in nests at depths from 1.3 to 2.0 m. Water temperature and the biological variables of fork length and age were as described in Table 4.1.

Most smallmouth nests approximated a circular shape. Two measurements of a nest's diameter were averaged when the "black-fry" were collected. The material in the bottom of the nest ranged from silt, to sand and broken shells, to stems of short Chara. Each nest was assigned a category from 1 to 3. These were ordered to reflect the increasing coraseness of the bottom of the nest. Nests with Chara contained the most interstitial spaces where offspring could reside undetected. Offspring in nests on silt were most exposed.

The modal height of Chara adjacent to each nest and the

Table 4.1 The name and description of the variables used to study reproductive success.

VARIABLE	DESCRIPTION
Date	The day of "black-fry" collection recorded as the number of days after May 15.
Water temperature	The water temperature of the Inner Bay on the day the "black-fry" are collected.
Windy hours	The total hours of wind in excess of 'Beaufort force 4' blowing from open water directions during offspring development.
Fork length	Fish length from snout to fork in caudal fin.
Age	Number of scale annular rings.
Nest diameter	Mean of maximum and minimum dimensions across nest.
Nest material	Categories of coarseness of materials in bottom of nest.
Chara height - nest	Modal height of *Chara* sp. adjacent to each nest.
Vegetation cover - nest	Portion of substrate covered by vegetation adjacent to each nest.
Chara height - general	Modal height of *Chara* sp. in general area of nest.
Vegetation cover - general	Portion of substrate covered by vegetation in general area of nests.
Sediment density	Grams of dry sediment per cm^3 of core sample in area around nests.
Water depth	Depth of water between the edge of each nest and the surface.

vegetation cover adjacent to each nest were measured using a 25 cm square quadrat. This was placed on four sides, abutting the edges of the nest. A mean Chara height and vegetation cover were calculated for each nest on the day the "black-fry" were collected.

The general habitat measurement of Chara height, vegetation cover and sediment density were not taken in relation to any specific nest. However they were restricted to the study site where the nest was located. Their value on the date of "black-fry" collection was used for each nest.

4.2.4 The analysis

I used multiple regression analysis (Snedecor and Cochran 1980) to determine the influence of several independent predictor variables on the single response variable, reproductive success. A major problem with using environmental variables was multicollinearity, where some or all of the 'independent' variables were intercorrelated. This arose either from causal relationships between variables or from similar responses to another unmeasured factor (Green 1979). To ensure the validity of the analytical results several statistical procedures were used. The purpose was twofold; to obtain a reduced subset of orthogonal predictor variables, and to evaluate the effect of studying reproductive success over two spawning seasons. A flow chart of the analyses used is in Figure 4.1.

The raw data were inspected using the MINITAB package (Ryan et al. 1976). The data were transformed to avoid violations of the heterogeneity of variance assumptions (Elliott 1977). The $\log_e$

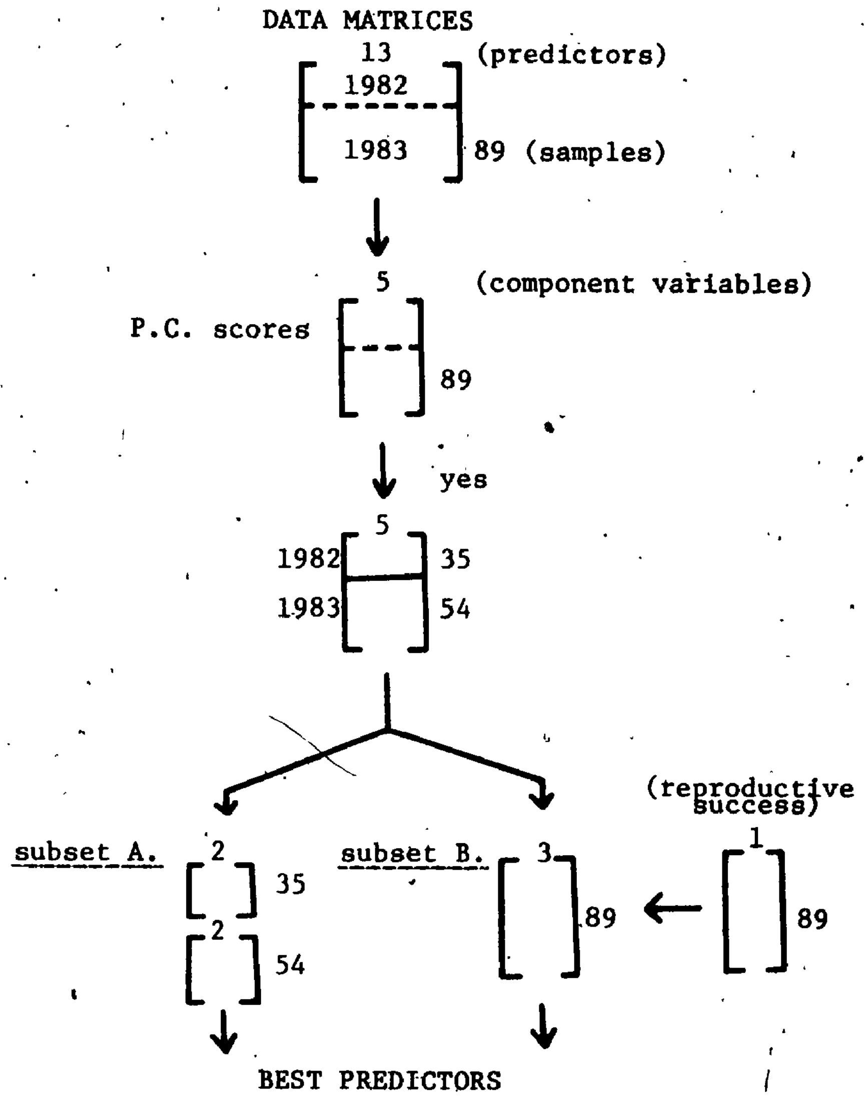
Figure 4.1 Flow diagram of analysis sequence used to determine influence of biological and physical factors on reproductive success. The procedures were done on the associated data matrices.

(*P.C.A. - principal components analysis.

**MANOVA - multivariate analysis of variance.

***D.F.A.-discriminant function analysis.)

OBJECTIVE	PROCEDURE
1. to produce: a) independent predictor variables b) reduced subset of variables	P.C.A.*
2. are there annual differences?	MANOVA**
3. which variables influence the annual difference?	D.F.A.***
4. what is the relationship between the predictors and reproductive success?	MULTIPLE REGRESSION



transformation was used to remove dependence of the variance on the mean for most variables. A square root transformation was applied to nest diameter to improve normality. The value for nest material remained untransformed because it was not a continuous variable and the variance was low.

Principal components analysis was used to convert the data to a set of new uncorrelated variables (Marriott 1974; Pimentel 1979; Green 1979). Because the new set of variables defined were then arranged in decreasing order of total variance contained, a reduced subset of variables was selected which accounted for most of the variability in the original data set. The components were extracted from a variance-covariance dispersion matrix using the MINITAB package. The effect of this analysis was to create a variable-by-PC matrix where each component was a linear additive function of the original variables.

The relative importance of the original variables to the new component variables was interpreted in two ways. The eigenvector (loading coefficient) represented the amount of variation in the original variable accounted for by the component. High eigenvector loadings of specific original variables were used to characterize the component. Additionally, structure coefficients (Sprules 1977; Chang 1981) were calculated. These were product-moment correlation coefficients between the original variables and the principal components. They showed the relative importance of the original variables to the principal components. Structure coefficients were calculated by:

$$a_{ij}\sqrt{l_j}/S_i$$

where a_{ij} was the eigenvector, l_j was the eigenvalue of the component and S_i was the standard deviation of variable X_i. Essentially the standard deviation was used to correct the weighting of a variable on each component.

Principal component scores were used as the data in subsequent analyses. These scores were calculated by multiplying the eigenvector matrix with the deviations-squared-cross-products matrix. Before proceeding with pooled 1982 and 1983 PC scores, annual differences in the new PC variables were tested using a multivariate analysis of variance on the partitioned scores. The MANOVA procedure in the Statistical Package for the Social Sciences (S.P.S.S.) (Hull and Nie 1981) was used. The significant annual variation found was examined further with discriminant function analysis (Marriott 1974; Klecka 1975; Pimentel and Frey 1978). This analysis determined how to best explain the differences between groups (years) based on the data (PC scores) from the new independent variables.

The final analysis was the multiple regression of reproductive success ("black-fry" counts) with the orthogonal predictor variables using the S.P.S.S. package (Kim and Kohout 1975). Essentially a linear model was constructed identifying the independent variables that provided the best possible prediction of the observed values of reproductive success. This proceeded on two subsets of the independent variables: one comprised of the variables that contained an annual effect and one where annual effects were weak or absent. These results were then synthesized into the best explanation of reproductive success in smallmouth bass.

4.3 Results

The number of smallmouth nests located in 1982 and 1983 with eggs or larvae and the proportion which successfully reached the "black-fry" stage are in Table 4.2. These success rates were compared using a test of equality of two percentages (Sokal and Rholf 1969). The test statistic:

$$t_s = \frac{\arcsin\sqrt{p_1} - \arcsin\sqrt{p_2}}{\sqrt{820.8\left(\frac{1}{n_1} + \frac{1}{n_2}\right)}}$$

gave a critical 't' of 8.52 which indicated a significant difference ($p < .001$) in the proportion of successful nests between years.

"Black-fry" were counted from 44 nests in 1982 and 74 nests in 1983. Data on all the predictor variables were available for 35 and 63 nests in the respective years. Only the complete samples were used in all analyses of reproductive success.

The average number of "black-fry" per nest in the two years was 640 and 1740. A one way analysis of variance indicated significantly more offspring ($p < .001$) per male smallmouth in 1983. The distribution of individual fry counts (reproductive success) is presented in Figure 4.2.

A summary of the means and variances for the original predictor variables used in the principal components analysis is in Table 4.3. Frequency distributions of these data are provided in Appendix 1. A reduced subset of 5 independent predictor variables (PC components)

Table 4.2 Synopsis of the total numbers of nests studied and the proportion of these which successfully produced "black-fry" during 1982 and 1983.

	Total nests with eggs or larvae	Percent of nests successful
1982	133	33
1983	85	87

Figure 4.2 Distribution of the numbers of "black-fry" collected in individual smallmouth nests in 1982 and 1983 (Reproductive success).

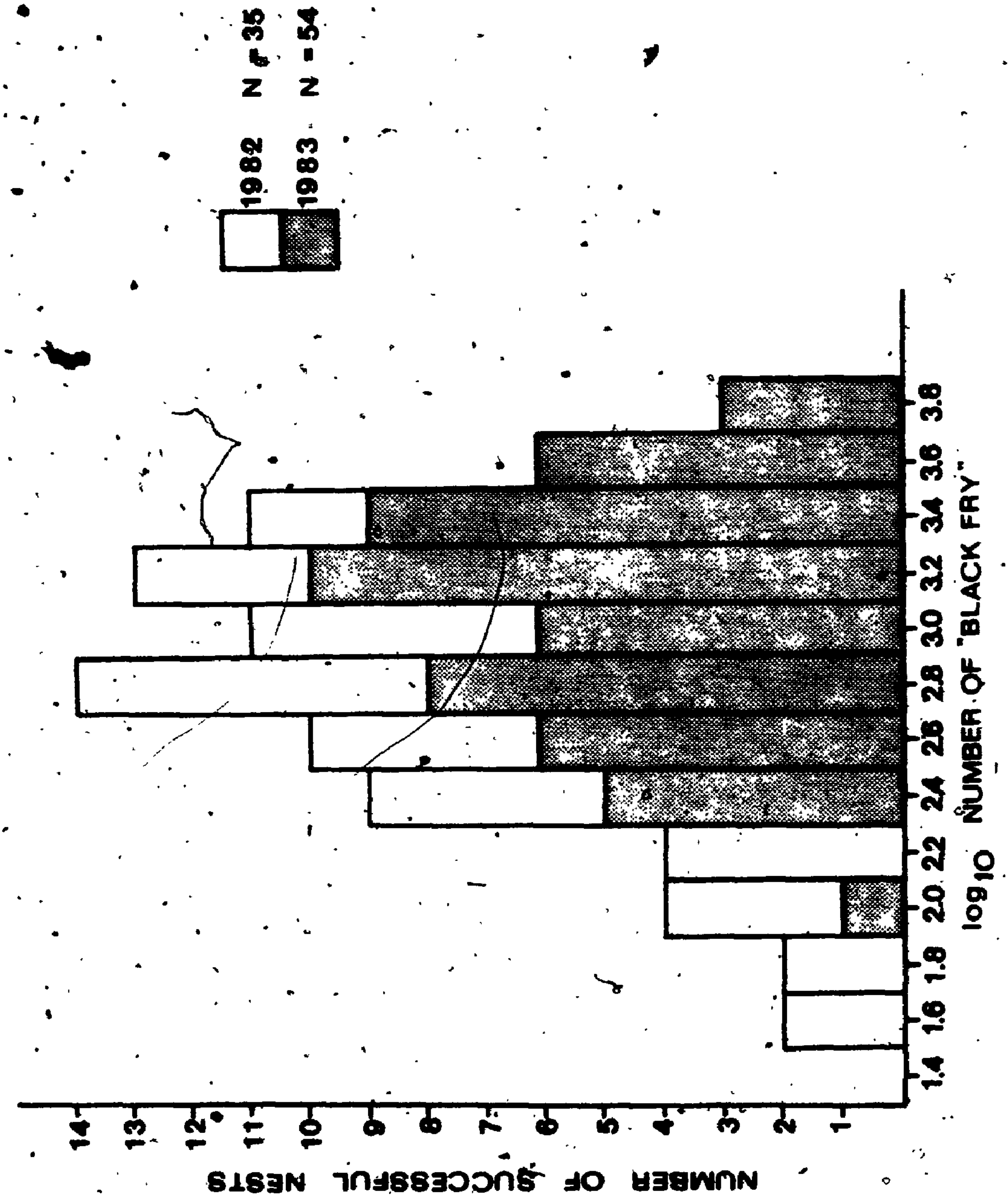

1982 N = 35
1983 N = 54
NUMBER OF SUCCESSFUL NESTS
1
2
3
4
5
6
7
8
9
10
11
12
13
14
1.4
1.6
1.8
2.0
2.2
2.4
2.6
2.8
3.0
3.2
3.4
3.6
3.8
log10 NUMBER OF "BLACK FRY"

Table 4.3 Transformations used, means and variances of raw and transformed data for the predictor variables.

VARIABLE	TRANSFORMATION	RAW DATA		TRANSFORMED DATA	
		$\bar{X}$	S^2	$\bar{X}$	S^2
Date	ln X	32.2	93.5	3.42	0.101
Water temperature	ln X	21.12	8.58	3.04	0.021
Windy hours	ln (X+1)	16.2	519.8	1.77	2.43
Fork length	$\log_{10}$ X	310.0	2314.0	2.49	.004
Age	ln X	4.85	1.93	1.54	.078
Nest diameter	$\sqrt{X}$	30.6	116.6	5.45	.859
Nest material	-	1.92	.687		
Chara height - nest	ln (X+1)	6.08	3.80	1.92	.085
Vegetation cover - nest	ln (X+1)	2.13	1.21	1.08	.132
Chara height - general	ln (X+1)	8.57	7.85	2.13	.078
Vegetation cover - general	ln (X+1)	2.24	.397	1.15	.045
Sediment density	ln (X+1)	2.05	.931	1.07	.031
Water depth	ln (X+1)	1.61	.025	0.96	.004

was selected from the original 13 biological and physical variables. These 5 accounted for 95.7 percent of the original variance. The results of the principal components analysis are in Table 4.4.

The corresponding structure coefficients on the first five components are in Table 4.5. The coefficient representations of a few original variables with low standard deviations were enhanced. For example, the importance of water temperature on the first component was increased. Similarly fork length became important on the fifth component. Those variables where importance increased most when structure coefficients were used, reflected natural correlations with the variables that had the highest coefficients (by both methods). The use of these two methods assisted in interpreting the major characteristic of the new orthogonal variables. The qualitative descriptions of these principal component variables are in Table 4.6.

The multivariate analysis of variance (MANOVA) to test annual differences in the 5 component variables calculated a Wilks lambda of .17574. This test statistic indicated significant annual differences ($p < .001$).

The multivariate assessment of how the 5 variables differed was provided by the discriminant function analysis, (direct method). The analysis produced one significant discriminant function axis ($p < .001$) between the groups (years). Box's "M" test indicated differences in the group covariance matrices, but this assumption is frequently violated in this analysis. Ninety-eight percent of the cases were correctly classified by group along the discriminant axis.

The standardized discriminant function coefficients in Table 4.7 indicate which variables contributed most to the discrimination

Table 4.4 Matrix of eigenvector loadings and percent of variance explained by first five principal components.

	PRINCIPAL COMPONENTS				
VARIABLE	1	2	3	4	5
Date	-.09	.03	.08	-.25	-.62
Fork length	.01	.01	-.02	.05	.11
Age	.05	.04	-.07	.16	.47
Nest diameter	.28	.90	-.32	.02	-.05
Nest material	-.17	-.27	-.92	-.21	-.07
Sediment density	-.02	-.04	-.11	.37	-.08
Chara ht. - nest	-.03	-.04	-.04	.37	-.21
Vegetation cover - nest	-.03	-.09	-.14	.59	.15
Water depth	-.01	.01	-.02	.05	-.04
Water temperature	-.06	.01	.02	-.05	-.04
Chara ht. - bkgd.	-.01	.01	-.01	.38	-.53
Vegetation cover - bkgd.	-.05	-.02	-.14	.30	-.11
Windy hours	.93	-.32	-.63	-.03	-.11
VARIANCE (eigenvalue)	2.71	.72	.65	.24	.09
% VARIANCE	58.7	15.6	14.0	5.2	2.0

Table 4.5 Structure (correlation) coefficients between the original variables and the first five principal components.

	PRINCIPAL COMPONENTS				
VARIABLE	1	2	3	4	5
Date	-.48	.08	.20	-.39	-.60
Fork length	.29	.12	-.22	.33	.50
Age	.33	.12	-.21	.29	.51
Nest diameter	.50	.82	-.28	.01	-.02
Nest material	-.34	-.28	-.89	-.12	-.02
Sediment density	-.12	-.14	-.32	.66	-.09
Chara ht. - nest	-.17	-.12	-.12	.63	-.22
Vegetation cover - nest	-.12	-.21	-.33	.80	.12
Water depth	.27	.16	-.23	.41	-.21
Water temperature	-.71	.06	.11	-.17	-.08
Chara ht. - bkgd.	-.09	.04	-.02	.68	-.58
Vegetation cover - bkgd.	-.38	-.07	-.05	.68	-.16
Windy hours	.99	-.18	-.03	.01	-.02

Table 4.6 Qualitative description of the PC variables using eigenvector loadings and structure coefficients.

	PRINCIPAL COMPONENT				
	1	2	3	4	5
Eigenvector loading	Wind	Nest Size	Nest Material	Vegetation-Sediment	Male age - time
Structure coefficient	Physical environment (Wind-water Temperature)	Nest Size	Nest Material	Vegetation-Sediment	Male size - time

Table 4.7 Standardized discriminant function coefficients. * indicates variables that contributed to annual differences.

VARIABLE	FUNCTION 1
PC 1 (Physical environment)	-1.175 *
PC 2 (Nest size)	.359
PC 3 (Nest material)	.244
PC 4 (Vegetation-sediment)	.333
PC 5 (Male size - time)	.609 *

between years. The large value of the coefficient for the physical environmental variable, i.e. wind, indicates the strong annual influence of this component. The coefficient for the fifth component variable suggested some annual differences in this minor axis. The low standardized coefficient values on the remaining components indicated they did not contribute differences between years. This interpretation was supported by the associated univariate F tests, where significant annual differences on PC1 ($p < .001$) and PC5 ($p = .02$) were found.

Analysis of the influence of the predictor variables on reproductive success proceeded in two parts. The subset of component variables for nest size, nest material and vegetation-sediment comprised one homogeneous (between years) group of predictors. Results of the multiple regression of "black-fry" with these variables are in Table 4.8. The second subset of component variables included the physical environment and male size-time components. Results of the multiple regression of "black-fry" with these variables are in Table 4.9.

Significant multiple regressions were obtained with both subsets of predictor variables. The wind or physical environmental influence accounted for the greatest proportion of variation in reproductive success. Its F value was significant ($p < .001$). The simple correlation of this variable with reproductive success was negative.

Among the remaining variables nest material also had a significant influence on the number of fry in a nest ($p = .016$). This simple correlation also had a negative sign.

Table 4.8 Multiple regression of numbers of "black-fry" with component variables that do not differ between years. N=89. * indicates significant F values.

VARIABLE	INDIVIDUAL F	SIGNIFICANCE	% VARIANCE	MULTIPLE F	SIGNIFICANCE
PC 2	1.37	.245	1.4	3.22	.027*
PC 3	6.09	.016*	6.4		
PC 4	2.21	.141	2.3		
			$\Sigma = 10.2$		

Table 4.9 Multiple regression of numbers of "black-fry" with component variables that vary between years. * indicates multiple F values.

VARIABLE	INDIVIDUAL F	SIGNIFICANCE	% VARIANCE	MULTIPLE F	SIGNIFICANCE
PC 1	19.46	< .001 *	18.2	10.5	< .001 *
PC 5	1.54	.219	1.4		
			$\Sigma = 19.6$		

The total variance in reproductive success that was explained by both multiple regressions was additive because the independent predictors were orthogonal. Together the physical and biological variables studied accounted for 29.8% of the variation in the numbers of "black-fry" in smallmouth bass nests.

4.4 Discussion

The numbers of "black-fry" that smallmouth bass produced were influenced by aspects of their environment. The total number of windy hours greater than Beaufort force 4, blowing over the nest during offspring development, had the largest influence of the variables measured. This was a negative relationship with fewer fry produced from nests subject to more windy hours. The detrimental effect of wind was mediated through the associated water movements (Wetzel 1975). At the water depths where nests in this study were found (1.3 - 2.1 m), the effect of water movement should have been homogeneously distributed following a short period of wind induced mixing (Prof. R. Boddour pers. comm.; Kit et al. 1980). Real effects on the nest were observed in the field on windy days. I observed that eggs and larvae in nests at 1.3, 1.5 and 2.0 m, were bounced in the bottom of the nest and distributed outside the boundary of the nest. The presence of undeveloped eggs in these nests on subsequent visits suggested this mechanical action damaged eggs. The wind-induced dispersal of offspring made them harder to defend by the male and therefore more available to predators.

The quantitative evaluation of the influence of wind on nesting centrarchids agreed with qualitative descriptions of its effect. Eipper (1975) speculated that year-class fluctuations in smallmouth bass might be sometimes caused by winds which are frequently correlated with below average temperatures. Kramer and Smith (1962) concluded that high winds and low temperatures were the first and second most important causes, respectively, of mortality to largemouth bass during the embryo-prolarval period. Miller and Kramer (1971) and Summerfelt (1975) also observed a relationship between high spawning success and stable weather in largemouth.

The material in the bottom of the smallmouth nest also influenced reproductive success. However, the negative sign of the simple correlation coefficient of "black-fry" with PC3 scores, indicated an inverse relationship which was opposite to that predicted. Category 3 of nest material was short Chara. On this coarsest of the nest substrates, eggs and larvae were most difficult for the observer to see, and therefore it was considered to be most effective in hiding offspring from predators. By comparison category 1 was open silt and clay on which the offspring were clearly most exposed. Three explanations for this relationship were available. First, offspring in the Chara were significantly harder to find and there was greater error in dredging up all the "black-fry". Secondly, female smallmouth may have contributed fewer eggs to a male in Chara as opposed to males with more clearly demarcated nests on bare clay. The third and most probable explanation was that the settlement of suspended silt on to the eggs and larvae in the protected Chara was less readily removed by parental fanning or water action. Paradoxically silt on these eggs and larvae may have suffocated more offspring than silt which settled into nests with bare bottoms.

The total proportion of the variance in reproductive success explained in this study (29.8%) initially appeared low. Two points need to be considered in this regard.

In other studies where reproductive success of fishes has been analyzed using multiple regression, higher proportions of the variation (r^2) were explained. Grant and Colgan (1982) explained 59% of the variation in the number of eggs a johnny darter, Etheostoma nigrum, obtained in a single nest. Schmale (1981) studied the number of clutches of eggs the bicolor damselfish, Eupomacentrus partitus, attracted and was able to account for 45% of the variance. Kodrick-Brown (1983) indexed reproductive success as the number of females mated by each male pupfish, Cyprinodon pecosensis. She accounted for 65% of the variation in reproductive success. In all these comparisons the r^2 explained was reported for predictor variables having significant F values in the multiple regression. These regression analyses of reproductive success have used various predictor variables relevant to the particular species studied. However, there was one major difference between these three studies and my own. Their reproductive success parameters were some measure of the maximum number of reproductive units obtained immediately following spawning, i.e. egg count, clutches of eggs or number of spawnings respectively. My evaluation of reproductive success was based on sampling of "black-fry" following the periods of egg and larval development. It was a more meaningful measure of how effectively a male contributed offspring to the next generation. It reflected in part his behavioural 'quality' in protecting his offspring. It also reflected some of the chance environmental influences that affect early survival. Consequently the r^2 of 29.8% was not as much an indication that the analysis did not effectively achieve its objective as it was a reflection of the stage of development at which reproductive success was evaluated.

One weakness of these cited studies on reproductive success was that they did not specifically assure the independence of their predictor variables. The reported r^2's may be somewhat artificially inflated due to partial correlation of two or more significant predictors.

Alternatively, my study may not have included a variable that was important to reproductive success. One potentially important influence that was not quantified and entered in the analysis was predation. Populations of rock bass, *A. rupestris*, and yellow perch, *P. flavescens*, were abundant in the study area and throughout the Bay (Whillans 1979). Predation of rock bass on smallmouth fry near nests was frequently observed. Schools of yellow perch occasionally fed in the vegetation near nests. Both species were chased from nests by parental male smallmouth. It was not likely that the influence of some other important physical environmental variable was completely omitted because of the general multicollinearity that exists between physical variables.

There were practical applications of studying reproductive success in smallmouth bass. Clearly there were good and poor spawning years. In a poor spawning year the number of nests successfully producing fry was relatively low. Higher numbers of offspring per successful nest were not produced to compensate. It would be wise for fish managers to restrict human disturbances of nesting male smallmouth, especially in good spawning years, in order to maximize recruitment to the exploitable population.

It was established that determination of a good spawning year can be done reasonably efficiently using existing weather records. The validity of this approach was based on the demonstrated importance of the influence of wind activity throughout the spawning season on successful reproduction.

CHAPTER 5 - RENESTING BY MALE SMALLMOUTH

5.1 Introduction

The high risk of reproductive failure in a year is a serious consequence of nesting in an environment with periodic storms and abundant predators. A male should respond to loss of his offspring in a manner compatible with maximizing his lifetime reproductive success. The alternatives include renesting that season or deferring the next reproductive effort until the following year. The best alternative depends on how good prospects are for continued survival and future reproduction (Williams 1966; Stearns 1976; Gadgill and Bossert 1970).

Several centrarchid species are capable of renesting one or more times in a season. Noltie (1982) observed that tagged male rock bass (A. rupestris) renested up to five times in a stream. Gross and Nowell (1980) reported 24 percent of lake spawning male rock bass renested and 33 percent of these were successful. Colonial breeding green sunfish (Lepomis cyanellus) constructed a series of nests, most within a meter of their previous nest (Hunter 1963). The multiple synchronous spawning periods in bluegills (L. macrochirus) and longear sunfish (L. megalotis) observed by Dominey (1981) and Bietz (1980) likely represented renesting efforts by the same males in these species..

Renesting in smallmouth bass following nest failure has been reported (Surber 1943; Cleary 1956; Henderson and Foster 1957), and renesting following successful reproduction also occurred (Pflieger 1966). Evidence from some smallmouth in Long Point Bay during 1982 indicated at least some of the males suffering natural mortality of their broods renested in their original territory. Two males individually recognized by body scars, successfully raised "black-fry" on their second and third nesting efforts respectively. These initial observations suggested a nest territory represented a valuable resource, as a new male occasionally moved into an abandoned nest.

The role of renesting in a male's annual reproductive effort was experimentally studied in the field in 1983. Searches for individually marked smallmouth undertaking a renesting effort were conducted at all study locations. However the objective was primarily focused on understanding the effectiveness of a subsequent reproductive effort in the territory used initially.

Several questions [illegible]evant to the objective were considered. Were there differences in the physical characteristics of nests used once compared to nests used twice? Did the number of "black-fry" on the first reproductive effort differ between these two groups of nests? How did the number of "black-fry" on each reproductive effort compare for individual males that renested? What biological characteristics distinguished renesting males?

5.2 Methods

Reproductive failure was simulated for 54 marked male smallmouth in 1983 by removing their offspring as they reached the "black-fry" stage. Nesting male smallmouth were caught underwater with a hand net and were individually marked with a unique combination of 3 holes (3 mm or 6 mm diameter) punched in the soft dorsal, anal or caudal fins. Observations of these fish did not indicate any changes in their behaviour after marking.

Measurements of male bass, reproductive success and the nesting environment were recorded as previously described (Chapter 4).

In order to study differences in the physical characteristics of nests used only once and nests where males renested, the data were partitioned into two groups. Male age and size were removed from analysis of these nests and considered separately. Principal components analysis was used (see Chapter 4) to create new orthogonal variables and provide a reduced subset of variables that contained most of the variance in the original data. Discriminant function analysis on PC scores of the component variables was used to distinguish the two groups of nests.

The number of "black-fry" raised on the first nesting effort might have influenced a male's decision to renest. I used a non-parametric Mann-Whitney 'U' test to test for differences in reproductive success on the first effort, between males that nested successfully only once and males that successfully renested. A non-parametric approach was chosen because of relatively low sample numbers (N=12,42), unequal sample sizes and non-normal distributions of both groups. When the conditions of parametric tests are not fulfilled, a non-parametric test is usually more powerful than its parametric equivalent (Elliott 1977).

The potential gain in reproductive success on the second effort may be an important factor when opting to renest. The numbers of "black-fry" in both efforts were compared with a paired t-test for the 10 males that produced "black-fry" on both efforts. This test assumed that the differences between the first and second "black-fry" counts were normally and independently distributed (Siegel 1956).

Finally, biological characteristics of renesting males were studied. Age and size (fork length) of renesting males were compared with single nesters using a Mann-Whitney 'U' test.

5.3 Results

Twelve of the 54 marked male smallmouth renested in the same territory a second time and 2 of these males renested a third time to successfully produce "black-fry". Forty-two nests were used only once.

Results of the principal components analysis of the measurements on all initial nests are presented in Table 5.1. Four component variables contained 94% of the variation in the original 11 physical variables. The major axis of variation in this analysis was most heavily influenced by nest material. Nest diameter and number of windy hours had the highest single eigenvector loadings on components 2 and 3 respectively. The associated structure coefficients are in Table 5.2.

PC scores on the first 4 components were calculated for each sample and used in the discriminant function analysis. Nests (groups) were coded for single nesting (N=42) or renesting (N=12). The analysis produced one significant discriminant function axis ($p=.002$) between the two groups. The group covariances matrices were equivalent ($p=.25$) using Box's M test. Meeting this assumption minimized concerns related to the sample sizes. Eighty-seven percent of the cases were correctly classified by this procedure along the discriminant axis.

The standardized discriminant function coefficients are in Table 5.3. The component variable PC3 (the seasonal windy hours - water temperature axis) provided most discrimination between groups of nests. The associated univariate F tests indicated significant differences between groups ($p=.001$) for PC3.

Table 5.1 Eigenvector loadings on first four principal components by the variables that characterize the 54 nests.

VARIABLE	PRINCIPAL COMPONENTS 1	2	3	4
Date	-.26	.09	.11	-.08
Nest diameter	-.17	-.94	.29	.02
Nest material	-.75	-.29	-.49	-.32
Sediment density	-.16	-.04	-.07	.53
Chara ht. - nest	-.06	-.01	-.14	.31
Vegetation cover - nest	-.14	-.08	-.13	.61
Water depth	-.01	-.01	-.02	.07
Water temperature	-.07	.06	.15	-.04
Chara ht. - bkgd.	-.08	.02	-.04	.31
Vegetation cover - bkgd.	-.04	-.02	-.04	.17
Windy hours	.58	-.12	-.77	-.05
VARIANCE (eigenvalue)	.92	.54	.48	.16
% VARIANCE	40.6	24.1	21.5	7.4

Table 5.2 Structure (correlation) coefficients of principal components with the original variables that characterize the 54 nests.

VARIABLE	PRINCIPAL COMPONENTS 1	2	3	4
Date	-.18	.49	.55	-.23
Nest diameter	.22	-.94	.27	.01
Nest material	-.86	-.26	-.41	-.16
Sediment density	-.48	-.10	-.15	.68
Chara ht. - nest	-.19	-.03	-.32	.42
Vegetation cover - nest	-.41	-.17	-.27	.74
Water depth	-.26	-.08	-.28	.55
Water temperature	-.48	.31	.73	-.12
Chara ht. - bkgd.	-.40	.06	-.16	.64
Vegetation cover - bkgd.	-.33	-.12	-.28	.61
Windy hours	.22	-.11	-.69	.02

Table 5.3 Standardized discriminant function coefficients on PC variables of physical characteristics of single and reused nests. * indicates variables that also differ significantly between groups on univariate F test.

VARIABLE	FUNCTION 1
PC 1 (Nest material)	-.494
PC 2 (Nest diameter)	.548
PC 3 (Windy hours)	.842 *
PC 4 (Vegetation sediment)	.016

The reproductive success of males on their first effort did not differ between groups (Table 5.4). This indicated a male's renesting in the same spot was not dependent on the number of offspring he reared to the "black-fry" stage on his first effort. However, renesting males were significantly older ($p=.0007$) and larger ($p=.0026$) than single nesters.

Reproductive success for renesting males was as good the second time as the first. A F_{max} test showed that the variance in numbers of "black-fry" of the 10 males sampled on both efforts was similar ($p > .05$). The paired t-test established that mean counts of "black-fry" for these males on their first and second efforts (1961 vs. 1656) were not significantly different ($p=.73$).

"Black-fry" were collected twice from only 10 of the 12 renesting males because 2 of these males were lost to anglers (as were 14 other nesting males). Evidence of angling mortality at some nests was clear. On one occasion a boat with a creel of smallmouth was chased from a patch of surface floats marking nests and several males that were nesting the previous day were taken. Some of the other angled nests lost the male before all the "black-fry" had disappeared. Losses to anglers never occurred in single nests but in groups of two or three as if a boat fished a patch of marked nests. Storms were never associated with males that were recorded as angling losses. An estimate of angling mortality on the nesting population was provided by the angling disappearance of 2 of the 12 marked renesting fish. Other males were angled and released between my visits to the study sites as indicated by fresh hook marks in the mandibles.

Table 5.4 Comparisons between males that spawned once (N=42) and those that spawned twice in the same territory (N=12). Differences were tested using the Mann-Whitney U test.

	Single Nester (N=42)	Renester (N=12)	p
Reproductive success on first effort (median number of "black-fry")	1327	1244	>.05
Age (years)	4	6	.0007
Fork length (mm)	283	348	.0026

5.4 Discussion

The establishment and defense of a nesting territory is a form of parental investment by the male (Baylis 1981; Ridley 1978). Renesting represents additional reproductive cost in time (i.e. lost feeding time) and energy (i.e. nest construction and defense) (Bell 1980). It is logical that a renesting male should take advantage of his expended investment by undertaking his second effort in the same territory.

Observations suggested that this was the practice, although the alternative of renesting elsewhere could not be rejected. Marked males, whose offspring were removed to simulate mortality were seen renesting only in the territory they initially occupied. They were never sighted during searches of nearby territories.

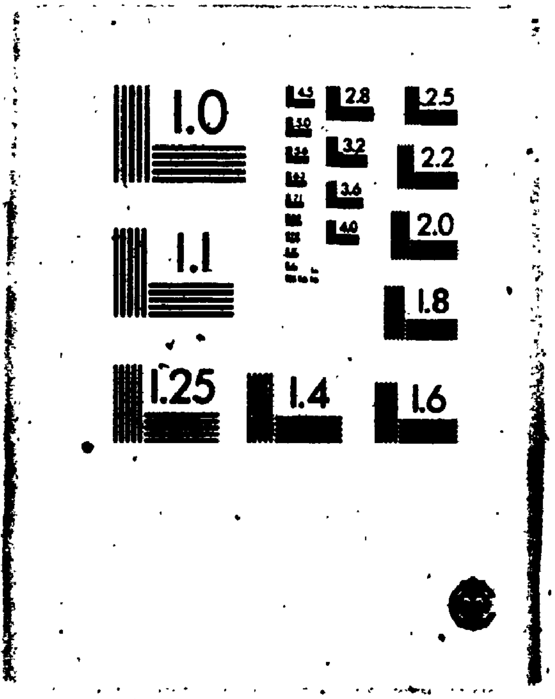
The data clearly showed that renesting males obtained a reproductive advantage in that season by comparison with failed males that did not renest. A renesting effort had a high probability of success, as all marked renesters produced "black-fry". The level of reproductive success did not significantly decrease on the second effort.

I considered several points to explain why only some males renested. The characteristics of the nesting environment on the initial effort were different for those males that responded to removal of offspring by renesting and those that did not. The differences between these two groups was most influenced by a physical environmental axis of variation. This variable reflected differences in nesting date, water temperature and wind regime. Most significantly, the mean water temperature in the bay was 23°C when mortality was simulated at nests used only once. Since the reported water temperature range for smallmouth spawning was 14 to 21°C (Miller 1975; Shuter et al. 1980) these established nests no longer provided suitable spawning habitat. By comparison the mean water temperature was 19° C when renesting males lost their first batch of "black-fry". These nests were still within a suitable temperature range for male smallmouth to respawn and resume their reproductive effort.

Renesting males also had a time advantage as I collected their "black-fry" an average of 6 days earlier than males that spawned once (day 28 vs. day 34). This extra time provided a sufficient period with appropriate nesting conditions, from which to expect a reasonable probability of successfully rearing a second brood of offspring.

Renesting males were distinguished biologically as the older and larger males. This agreed with the theory that reproductive effort increases with age (Gadgil and Bossert 1970; Williams 1966). As a fish gets older its future reproductive value decreases and the option of investing more in current reproductive effort becomes more profitable (Pianka and Parker 1975). The probability of survival past 6 years for smallmouth males in Long Point Bay did not appear to be high. Only 5 percent of spawners in both 1982 and 1983 were older than 7 years and the oldest nesting fish was 9 years old. This restricted age structure was presumed to be due to the high exploitation by recreational angling, since smallmouth bass are known to reach much older ages in Ontario (Tester 1932; Scott and Crossman 1973).

2 OF/DE 2



The possibility that smaller and later spawning males renested at new sites having cooler water temperatures outside the Inner Bay was unlikely. Following the previous logic the younger males should have benefitted by avoiding additional renesting costs in order to enhance growth and/or survival to a larger size the next season. The initial nesting effort in smaller fish has already provided two significant benefits. These were the reproductive experience which may enhance future success - and the opportunity to begin contributing to lifetime fitness earlier.

CHAPTER 6 - CONCLUSION

Data on the reproductive behaviour and ecology of smallmouth bass in a large natural lake was gathered by this research. The use of SCUBA to observe smallmouth in Long Point Bay, Lake Erie, during their breeding period was an effective approach. A catalogue of the behaviour patterns displayed during the reproductive period was compiled. Several previously unreported behaviours including alert display, crossover, inter-quiver pause and tail beat were observed and described. Other behaviour, i.e. parental guarding, was refined into units of fanning, patrolling and defending. This facilitated understanding the efficiency of behavioural organization and the interaction of male and female behaviours during the spawning cycle. The observation of a number of complete spawning sequences provided initial insight into a mating system of nesting smallmouth, where males may exercise selectivity in choosing mates.

Reproductive success, or the number of offspring a male smallmouth reared to the "black-fry" stage, was used as an operational estimator of fitness. The influence on reproductive success of a number of factors in the nesting male's environment were evaluated. Principal components analysis was used to derive independent predictor variables that were linear additive components of the originally measured variables. Multiple regression analysis of "black-fry" with a reduced subset of independent predictors indicated that the accumulated hours of wind (having a force greater than Beaufort force 4) that blew during offspring development had the largest significant influence on reproductive success. The numbers of "black-fry" were lower in nests subject to windier regimes. The type of material in the bottom of the nest also significantly influenced reproductive success, but to a lesser degree. A clay/silt nest substrate was more productive than the coarser sand or short vegetation. Together both these variables accounted for 29.8% of the variance in the numbers of "black-fry" of male smallmouth. The value of these results was made clear in the context of 3 important points. First, all the predictor variables were made completely independent by the analysis which meant that no variation was explained more than once. Secondly, reproductive success of the males was evaluated at the "black-fry" stage. This followed a period during which the quality of the male was tested, both in his attractiveness to females and in his ability to protect his offspring. Finally, the high level of predation observed around smallmouth nests may have caused significant variation in "black-fry" numbers among nests. This was not measured at individual nests during this study.

The proportion of nests receiving eggs that successfully produced "black-fry" varied significantly between years. This ranged from 33 to 88 percent. The average number of "black-fry" per successful nest was significantly lower in a 'poor' year.

Renesting in their same territory by male smallmouth was studied in 54 marked fish during 1983. It occurred in response to the loss of their first brood. Offspring mortality was simulated by removing "black-fry" from nests. Twenty-two percent of marked males undertook a second effort in their original territory. No tagged males were found nesting elsewhere, although this alternative cannot be firmly rejected. Renesting males were older and larger than single nesters. Their average numbers of offspring did not differ significantly between efforts. Renesting represented an effective way to minimize reproductive failure in one season.

REFERENCES

Adams, C.C. and T.L. Hankinson, 1928. The ecology and economics of Oneida Lake fish. Roosevelt Wild Life Annals 1 (3,4): 235-248.

Altmann, J., 1974. Observational study of behaviour: sampling methods. Behaviour 49 (3-4): 227-265.

Bagenal, T.B. and F.W. Tesch, 1978. Age and growth. In: T.B. Bagenal (ed.) Methods for assessment of fish production in fresh waters. I.B.P. Handbook #3, p.101-136.

Bain, M.B. and L.A. Helfrich, 1983. Role of male parental care in survival of larval bluegills. Trans. Am. Fish. Soc. 112: 47-52.

Baylis, J.R., 1981. The evolution of parental care in fishes, with reference to Darwin's rule of male sexual section. Env. Biol. Fish 6 (2): 223-251.

Beeman, H.W., 1924. Habits and propagation of the small-mouthed black bass. Trans. Am. Fish. Soc. 54: 92-107.

Bell, G., 1980. The costs of reproduction and their consequences. Am. Nat. 116: 45-76.

Bennett, G.W. and W.F. Childers, 1957. The smallmouth bass Micropterus dolomieui in warm-water ponds. J. Wildl. Mgmt. 21(4): 414-424.

Bennett, G.W., 1965. The environmental requirements of centrarchids with reference to largemouth bass, smallmouth bass and spotted bass. In: C.M. Tarzwell (ed.) Biological problems in water pollution - 3rd seminar 1962. U.S. Public Health Service Publ. No. 999-WP-25, pp. 156-160.

Berst, A.H. and H.R. McCrimmon, 1966. Comparative summer limnology of Inner Long Point Bay, Lake Erie, and its major tributary. J. Fish. Res. Bd. Can. 23 (2): 275-291.

Bietz, B., 1980. The adaptive significance of territorial aggregation in longear sunfish. Ph.D. thesis University of Western Ontario, London, Canada, 126 pp.

Bietz, B.F., 1981. Habitat availability, social attraction and nest distribution patterns in longear sunfish. Env. Biol. Fish. 6 (2): 193-200.

Breder, C.M., 1936. The reproductive habits of North American sunfishes (Family Centrarchidae). Zoologica 21 (1): 1-47.

Breder, C.M. and D.E. Rosen, 1966. Modes of reproduction in fish. The Natural History Press, Garden City, N.Y., 941 pp.

Brown, J.L., 1975. The evolution of behaviour. W.N. Norton & Co., New York, 761 pp.

Chang, W.Y.B., 1981. Advantages of eigenvectors over structure coefficients as indicators for selecting the response variables in principal components. Can. J. Fish. Aquat. Sci. 38: 1298-1299.

Christie, W.J. and H.A. Regier, 1973. Temperature as a major factor influencing reproductive success of fish - two examples. Rapp. P-V Reun. Cons. Int. Explor. Mer 164: 208-218.

Cleary, R.E., 1956. Observations on factors affecting smallmouth bass production in Iowa. J. Wildl. Mgmt. 20 (4): 353-359.

Clady, M.D., 1975. Early survival and recruitment of smallmouth bass in northern Michigan. J. Wildl. Mgmt. 39(1): 194-200.

Coble, D.W., 1975. Smallmouth bass. In: R.H. Stroud and H. Clepper (eds.) Black bass, biology and management. Sports Fishing Institute, Washington, D.C., pp. 21-33.

Dominey, W.J., 1981. Anti-predator function of bluegill sunfish nesting colonies. Nature 290: 585-588.

Dominey, W.J., 1981. Maintenance of female mimicry as a reproductive strategy in bluegill sunfish (*Lepomis macrochirus*). Env. Biol. Fish. 6 (1): 59-64.

Eipper, A.W., 1975. Engironmental influences on the mortality of bass embryos and larvae. In: R.H. Stroud and H. Clepper (eds.) Black bass biology and management. Sports Fishing Institute, Washington, D.C., pp. 295-305.

Elliott, J.M., 1977. Some methods for the statistical analysis of samples of benthic invertebrates (2nd. ed.). Sci. Publ. 25, Freshwater Biological Association. Ferry House, U.K. 160 pp.

Fry, F.E.J. and K.E.F. Watt, 1955. Yields of year classes of the smallmouth bass hatched in the decade of 1940 in Manitoulin Island waters. Trans. Am. Fish. Soc. 85: 135-143.

Gadgil, M. and W.H. Bossert, 1970. Life historical consequences of natural selection. Am. Nat. 104: 1-24.

Goff, G.P., 1984. Brood care of longnose gar (*Lepisosteus osseus*) by smallmouth bass (*Micropterus dolomieui*). Copeia 1984 (1): 149-152.

Goff, G.P., (In press). Environmental influences on annual variations in nest success of smallmouth bass, *Micropterus dolomieui*, in Long Point Bay. Env. Biol. Fish.

Grant, J.W.A. and P. Colgan, 1982. Reproductive success and mate choice in the johnny darter (Etheostoma nigrum) (Pisces Percidae). Can. J. Zool. 61: 437-446.

Green, R.H., 1979. Sampling design and statistical methods for environmental biologists. John Wiley & Sons, Toronto. 257 pp.

Gross, M.R., 1982. Sneakers, satellites and parentals: polymorphic mating strategies in North American sunfishes. Z. Tierpsychol. [illegible]: 1-26.

Gross, M.R[illegible] 1984. Sunfish, salmon and the evolution of alternative reproductive strategies and tactics in Fishes. In: R.J. Wotton and G. Potts (eds.) Fish reproduction: strategy and tactics Academic Press, London, 55-75.

Gross, M.R. and E.L. Charnov, 1980. Alternative male life-histories in bluegill sunfish. Proc. Natl. Acad. Sci. 77 (11): 6937-6940.

Gross, M.R. and W.A. Nowell, 1980. The reproductive biology of rock bass, Ambloplites rupestris, (Centrarchidae) in Lake Opinicon, Ontario. Copeia (3): 482-494.

Hamilton, W.D., 1964. The genetical evolution of social behaviour I. J. Theoret. Biol. (7): 1-16.

Heathcote, I.W., 1981. Major physical features of Long Point Bay and its watershed. J. Great Lakes Res. 7 (2): 89-95.

Henderson, C. and R.F. Foster, 1957. Studies of smallmouth black bass (Micropterus dolomieui) in the Columbia River near Richland, Washington. Trans. Am. Fish. Soc. 86 (1956): 112-127.

Hjort, J., 1926. Fluctuations in the year classes of important food fishes. J. Cons. Int. Explor. Mer 1 (1): 5-38.

Hubbs, C.L. and R.M. Bailey, 1938. The smallmouthed bass. Bull. Cranbrook Inst. Sci. 10: 1-89.

Hunter, J., 1963. The reproductive behaviour of the green sunfish, <u>Lepomis cyanellus</u>. Zoologica 48 (2): 13-24.

James, M.C., 1930. Spawning reactions of smallmouthed bass. Trans. Am. Fish. Soc. 60: 62-63.

Keenleyside, M.H.A., 1972. Intraspecific intrusions into nests of spawning longear sunfish (Pisces: Centrarchidae). Copeia 2: 272-278.

Keenleyside, M.H.A., 1978. Reproductive isolation between pumpkinseed (<u>Lepomis gibbosus</u>) and longear sunfish (<u>L. megalotis</u>) (Centrarchidae) in the Thames River, Southwestern Ontario. J. Fish. Res. Bd. Can. 35 (1): 131-135.

Keenleyside, M.H.A., 1979. Diversity and adaptation in fish behaviour. Springer-Verlag, New York, 208 pp.

Kelso, J.P. and R. Frank, 1974. Organochlorine residues, mercury, copper and cadmium in yellow perch, white bass and smallmouth bass, Long Point Bay, Lake Erie. Trans. Am. Fish. Soc. 103 (4): 577-581.

Kim, J.O. and F.J. Kohout, 1975. Multiple regression analysis: subprogram regression. In: N.H. Nie, C.H. Hull, J.G. Jenkins, K. Steinbrenner and D.H. Bent (eds.) SPSS: statistical package for the social sciences McGraw-Hill Book Co., New York, 320-367.

Kit, E., E. Berent and M. Vajda, 1980. Vertical mixing induced by wind and a rotating screen in a stratified fluid in a channel. J. of hydraulic Res. 18 (1): 35-57.

Klecka, W.R., 1975. Discriminant analysis. In: N.H. Nie, C.H. Hull, J.G. Jenkins, K. Steinbrenner and D.H. Bent (eds.) SPSS: statistical package for the social sciences McGraw-Hill Book Co., New York, 434-467.

Kodric-Brown, A., 1983. Determinants of male reproductive success in pupfish (Cyprinodon pecosensis). Anim. Behav. 31: 128-137.

Kohli, B. and R. Farooqui, 1980. Nanticoke water movements 1967-1978. Ont. Min. of Environemnt, Toronto, 65 pp.

Kramer, R.H. and L.L. Smith, 1962. Formation of year classes in largemouth bass. Trans. Am. Fish. Soc. 91 (1): 29-41.

Kraus, E.B., 1974. Wind and dynamics tables. In: F.G.W. Smith (ed.) Handbook of marine science, Vol. 1 CRC Press, Cleveland, Ohio, 175-269.

Krebs, J.R., 1978. Optimal foraging: decision rules for predators. In: J.R. Krebs and N.B. Davies (eds.) Behavioural ecology: an evolutionary approach. Blackwell Scientific Publication, London, 23-63.

Leach, J., 1981. Comparative limnology of inner Long Point Bay, Lake Erie, and adjacent waters of the Outer Bay. J. Great Lakes Res. 7 (2): 123-129.

Lehner, P.N., 1979. Handbook of ethological methods. Garland STPM Press, New York, 403 pp.

Loiselle, P.V., 1982. Male spawning-partner preference in an arenabreeding teleost, (Cyprinodon macularius californiensis), Girard (Antherinomorpha cyprinodontidae). Am. Nat. 20 (6): 721-732.

Loiselle, P.V. and G.W. Barlow, 1978. Do fish lek like birds? In: E.S. Reese and F.J. Lightner (eds.) Contrasts in behaviour. Wiley & Sons, Toronto, 31-75.

MacLean, N.G. and G.C. Teleki, 1977. Homing behaviour of rock bass (Ambloplites rupestris) in Long Point Bay, Lake Erie. J. Great Lakes Res. 3 (3-4): 211-214.

Marler, P., 1975. Observation and description of behaviour. In: E.O. Price and A.W. Stokes (eds.) Animal behaviour in laboratory and field, 2nd. edition. W.H. Freeman & Co., San Fransisco, 2-4.

Marriott, F.H.C., 1974. The interpretation of multiple observations. Academic Press, New York, 117 pp.

Miller, K.D. and R.H. Kramer, 1971. Spawning and early life history of largemouth bass (Micropterus salmoides) in Lake Powell. In: G.E. Hall (ed.) Reservoir fisheries and limnology. Spec. Publ. #8 Am. Fish. Soc., Washington, 73-83.

Miller, R.J., 1975. Comparative behaviour of centrarchid basses. In: R.H. Stroud and H. Clepper (eds.) Black bass biology and management. Sport Fishing Institute, Washington, D.C., 85-94.

Myrberg, A.A. Jr., 1972. Ethology of the bicolor damselfish, Eupomacentrus partitus (Pisces: Pomacentridae): a comparative analysis of laboratory and field behaviour. Anim. Behav. Monogr. 5 (3): 197-283.

Neves, R.J., 1975. Factors affecting fry production of smallmouth bass (Micropterus dolomieui) in South Branch Lake, Maine. Trans. Am. Fish. Soc. 104: 83-87.

Nie, N.H. and C.H. Hull, 1981. SPSS update 7-9: new procedures and facilities for releases 7-9. McGraw-Hill Book Co., New York, 402 pp.

Noltie, D.B., 1982. The reproductive ecology and behaviour of stream-dwelling rock bass Ambloplites rupestris (Rafinesque). M.Sc. thesis, University of Western Ontario, London, Canada, 241 pp.

Perrone, M., 1978. Mate size and breeding success in a monogamous cichlid fish. Env. Biol. Fish. 3 (2): 193-201.

Pflieger, W.L., 1966. Reproduction of the smallmouth bass (Micropterus dolomieui) in a small Ozark stream. Am. Midland Natur. 76 (2): 410-418.

Pianka, E.R. and W.S. Parker, 1975. Age-specific reproductive tactics. Am. Nat. 109: 453-464.

Pimentel, R.A., 1979. Morphometrics the multivariate analysis of biological data. Kendall/Hunt Publishing Co., Dubrique, Iowa, 276 pp.

Pimentel, R.A. and D.F. Frey, 1978. Multivariate analysis of variance and discriminant analysis. In: P.W. Colgan (ed.) Quantitative ethology. John Wiley & Sons, New York, pp. 247-274.

Reid, D.J., 1981. A survey of spawning bass in Long Point Bay during 1979. Unpublished Ont. Min. Nat. Res. Rept., S.W. Region, 36 pp.

Reighard, J.E., 1905. The breeding habits, development and propagation of the black bass (*Micropterus dolomieui* Lacepede and *Micropterus salmoides* Lacepede). Mich. Fish. Comm. Bull. 7: 1-73.

Ridley, M., 1978. Paternal care. Anim. Behav. 26: 904-932.

Robbins, W.H. and H.R. MacCrimmon, 1974. The black bass in America and overseas. Biomanagement and Research Enterprises, Ontario, 196 pp.

Romero, J. and R.C. Allen, 1975. Underwater observations of largemouth bass spawning and survival in Lake Mead. In: R.H. Stroud and H. Clepper (eds.) Black bass biology and management. Sports Fishing Institute, Washington, D.C., pp 104-112.

Ryan, T.A. Jr., B.L. Joiner and B.F. Ryan, 1976. Minitab student handbook. Duxbury Press, North Scituate, Mass., 341 pp.

Schmale, M.C., 1981. Sexual selection and reproduction in males of bicolor damselfish, *Eupomacentrus partitus* (Pisces: Pomacentridae). Anim. Behav. 29: 1172-1184.

Schneider, C.P., 1971. SCUBA observations of spawning smallmouth bass. N.Y. Fish & Game Jour. 18 (2): 112-116.

Scott, W.B. and E.J. Crossman, 1973. Freshwater fishes of Canada. Fish. Res. Bd. Can. Bull. 184, 966 pp.

Shuter, B.J., J.A. MacLean, F.E.J. Fry and H.A. Regier, 1980. Stochastic simulation of temperature effects on first-year survival of smallmouth bass. Trans. Am. Fish. Soc. 109: 1-34.

Siegel, S., 1956. Nonparametric statistics for the behavioural sciences. McGraw-Hill Book Co., Toronto, 312 pp.

Smith, D.W., 1979. Ecological isolation between Aythya species at Long Point Bay, Ontario. M.Sc. thesis, University of Western Ontario, London, Canada, 65 pp.

Snedecor, G.W. and W.G. Cochran, 1980. Statistical methods (7th ed.). Iowa State Univ. Press, Ames, Iowa, 507 pp.

Sokal, R.R. and F.J. Rohlf, 1969. Biometry: the principles and practice of statistics in biological research. W.H. Freeman and Co., San Francisco, 776 pp.

Sprules, W.G., 1977. Crustacean zooplankton communities as indicators of limnological conditions: an approach using principal component analysis. J. Fish. Res. Bd. Can. 34: 962-975.

Stearns, S.C., 1976. Life history tactics: a review of the idea. Quart. Rev. Biol. 51 (1): 3-47.

Summerfelt, R.C., 1975. Relationship between weather and year-class strength of largemouth bass. In: R.H. Stroud and H. Clepper (eds.), Black bass biology and management. Sports Fishing Institute, Washington, D.C., pp 166-174.

Surber, E.W., 1943. Observations on the natural and artificial propagation of the smallmouth black bass, Micropterus dolomieui. Trans. Am. Fish. Soc. 72: 233-245.

Sztramko, L. and G.C. Teleki, 1977. Annual variations in the fecundity of yellow perch from Long Point Bay, Lake Erie. Trans. Am. Fish. Soc. 106: 578-582.

Tester, A.L., 1930. Spawning habits of smallmouthed black bass in Ontario waters. Trans. Am. Fish. Soc. 60: 53-61.

Tester, A.L., 1932. Rate of growth of the smallmouthed black bass (Micropterus dolomieui) in some Ontario waters. Publication of Ontario Fisheries Research Laboratory #47, Univ. of Toronto Press, pp. 207-227.

Vogele, L.E. and W.C. Rainwater, 1975. Use of brush shelters as cover by spawning black basses (Micropterus) in Bull Shoals Reservoir. Trans. Am. Fish. Soc. 104: 264-269.

Wetzel, R.G., 1975. Limnology. W.B.Saunders Co., Toronto, 743 pp.

Whillans, T.H., 1979. Historic transformations of fish communities in three Great Lakes bays. J. Great Lakes Res. 5 (2): 195-215.

Williams, George C., 1966. Adaptation and natural selection: a critique of some current evolutionary thought. Princeton University Press, 307 pp.

Williams, G.C., 1975. Sex and evolution. Monographs in population biology #8. Princeton University Press, Princeton, 200 pp.

Winemiller, K.O. and D.H. Taylor, 1982. Smallmouth bass nesting behaviour and nest site selection in a small Ohio stream. Ohio J. Sci. 82 (5): 266-273.

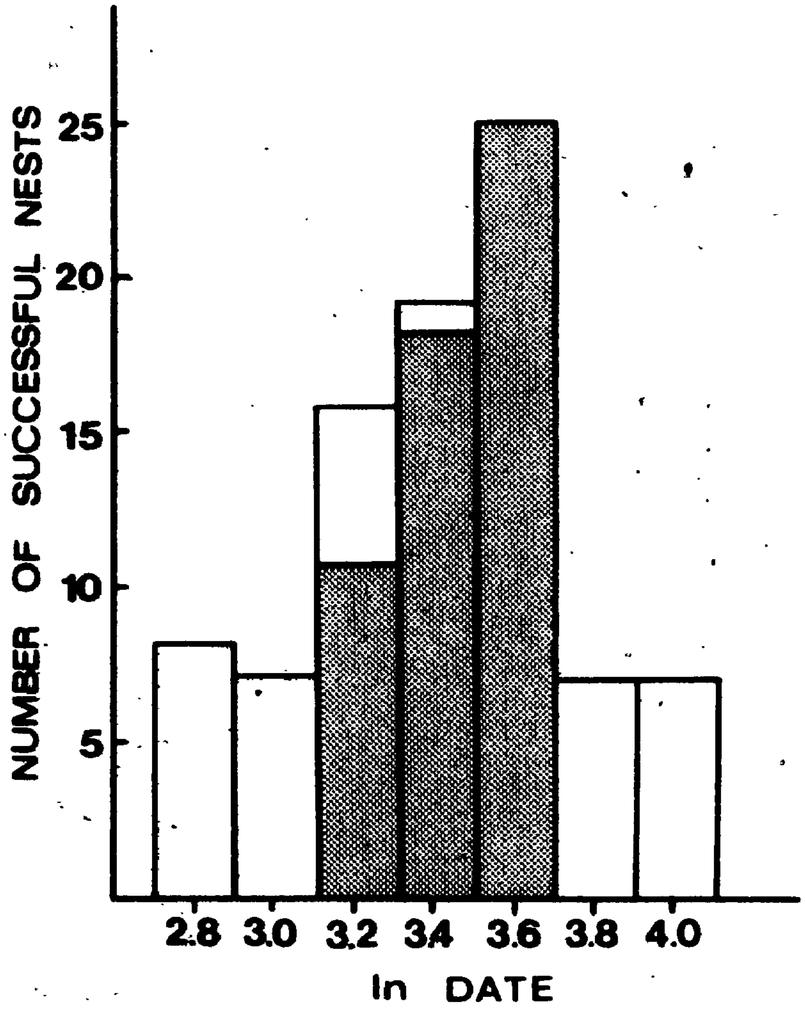
Wittenberger, J.F., 1981. Animal social behaviour. Duxbury Press, Boston, 722 pp.

APPENDIX 1

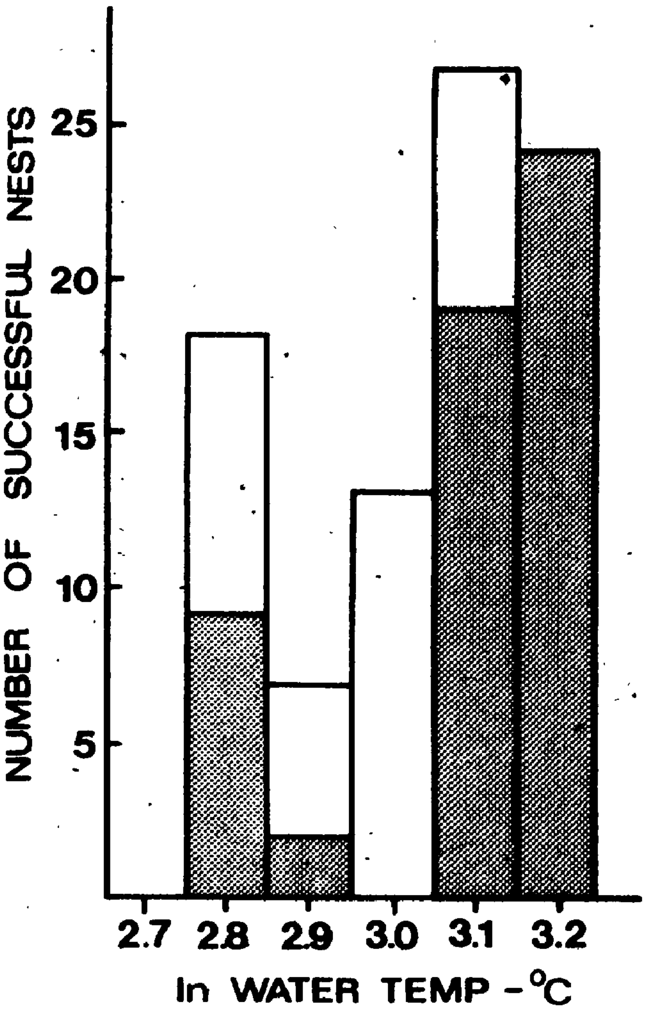
Distributions of 13 predictor variables measured for successful smallmouth bass. Stippled bars are 1983 data; open bars are 1982 data.

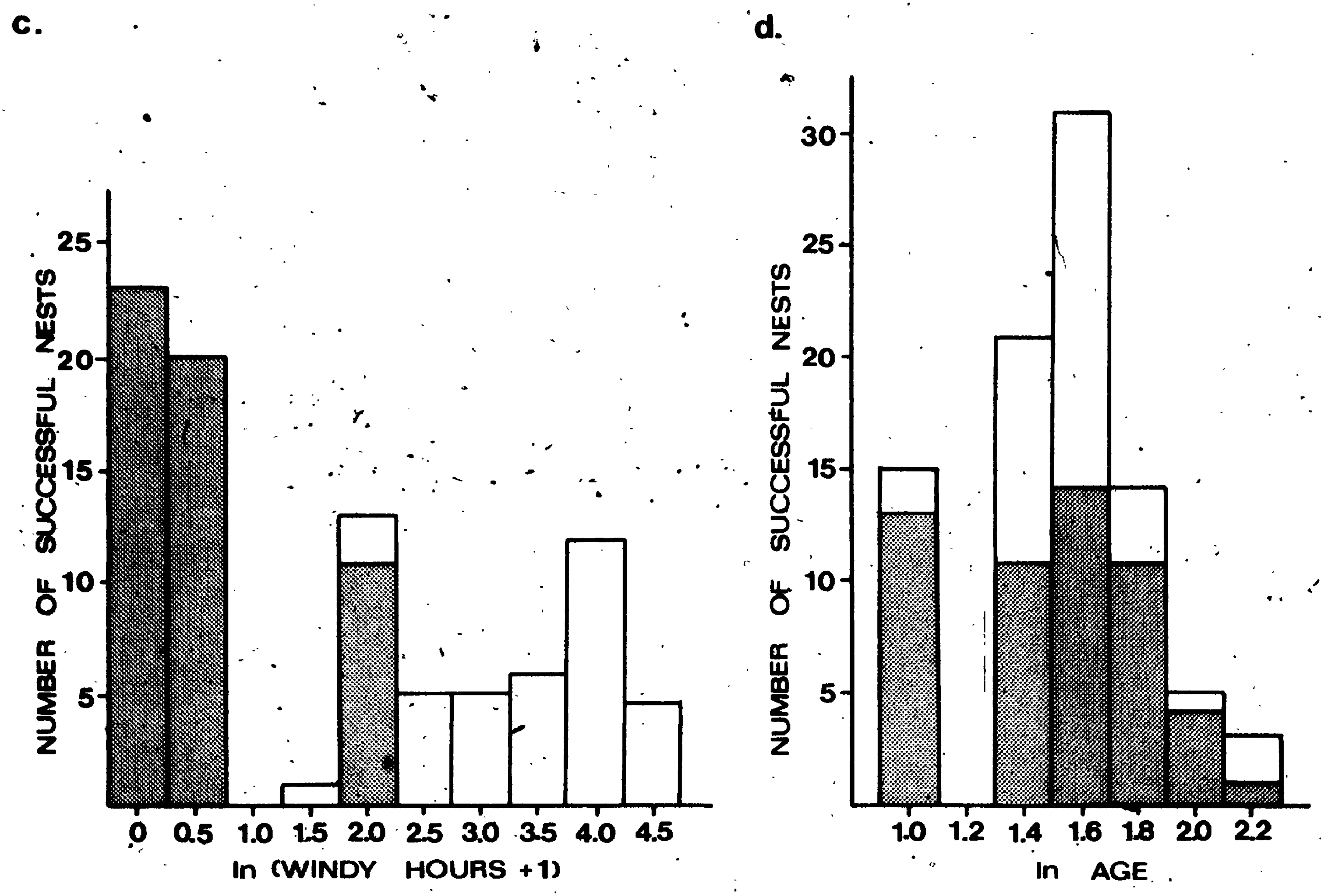
1 a	Date
1 b	Water temperature
1 c	Windy hours
1 d	Age
1 e	Fork length
1 f	Nest diameter
1 g	Nest material
1 h	Sediment density
1 i	Modal height of <u>Chara</u> at nest
1 j	Vegetation cover at nest
1 k	Modal height of <u>Chara</u> in general area
1 l	Vegetation cover in general area
1 m	Water depth

a.

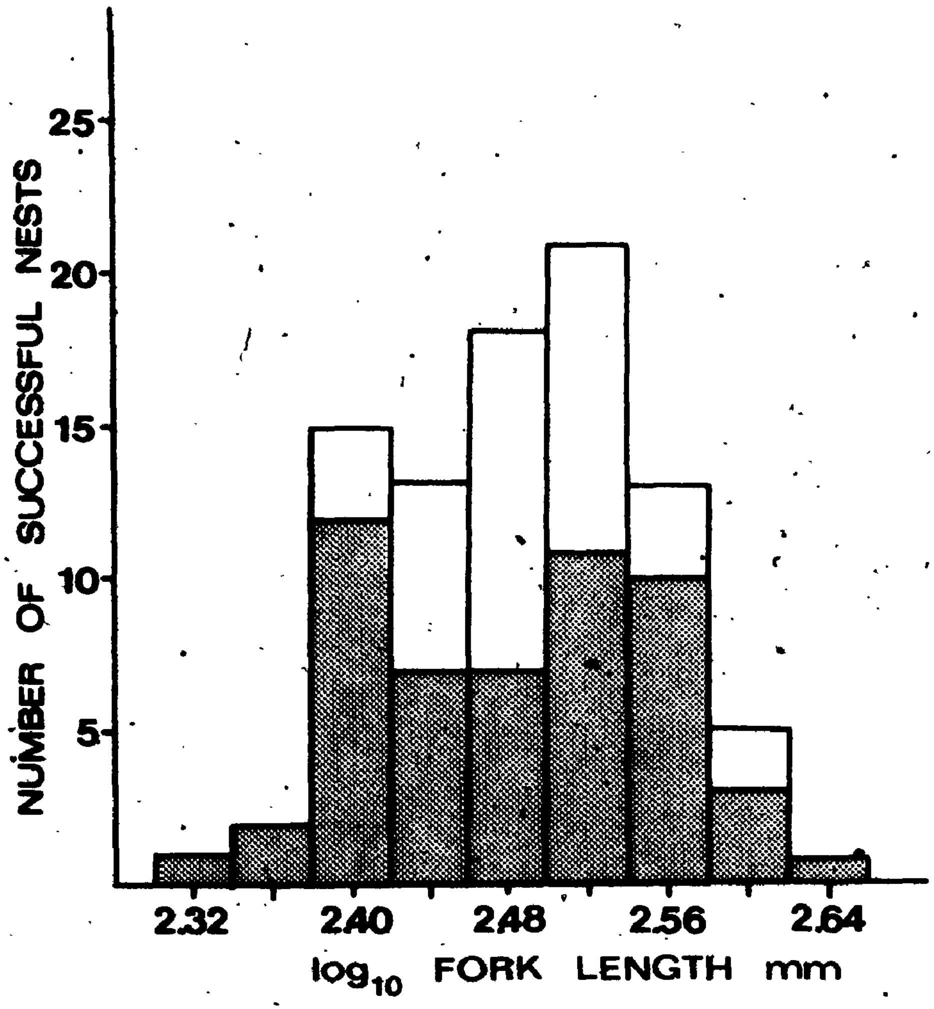

NUMBER OF SUCCESSFUL NESTS
5
10
15
20
25
2.8
3.0
3.2
3.4
3.6
3.8
4.0
ln DATE

b.

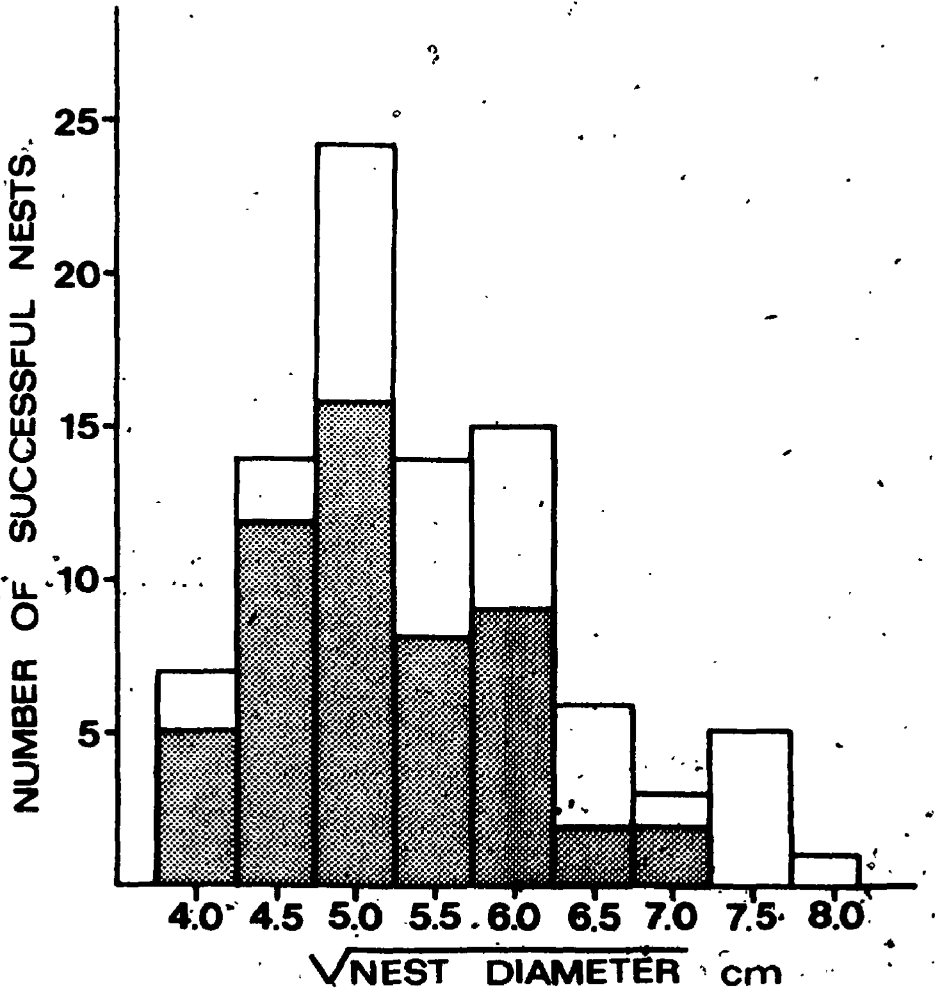

NUMBER OF SUCCESSFUL NESTS
5
10
15
20
25
2.7
2.8
2.9
3.0
3.1
3.2
ln WATER TEMP - °C


c.
NUMBER OF SUCCESSFUL NESTS
5
10
15
20
25
0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
4.5
ln (WINDY HOURS +1)
d.
NUMBER OF SUCCESSFUL NESTS
5
10
15
20
25
30
1.0
1.2
1.4
1.6
1.8
2.0
2.2
ln AGE

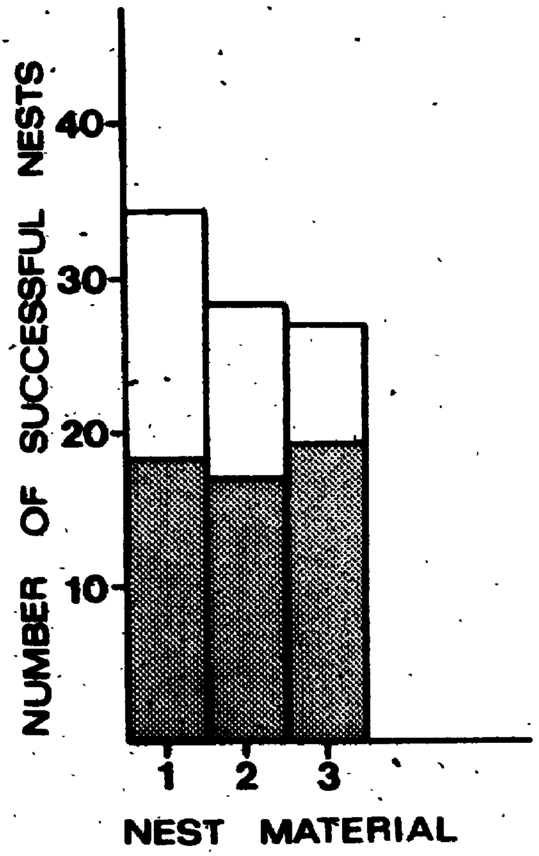
e.


NUMBER OF SUCCESSFUL NESTS
25
20
15
10
5
2.32
2.40
2.48
2.56
2.64
log$_{10}$ FORK LENGTH mm

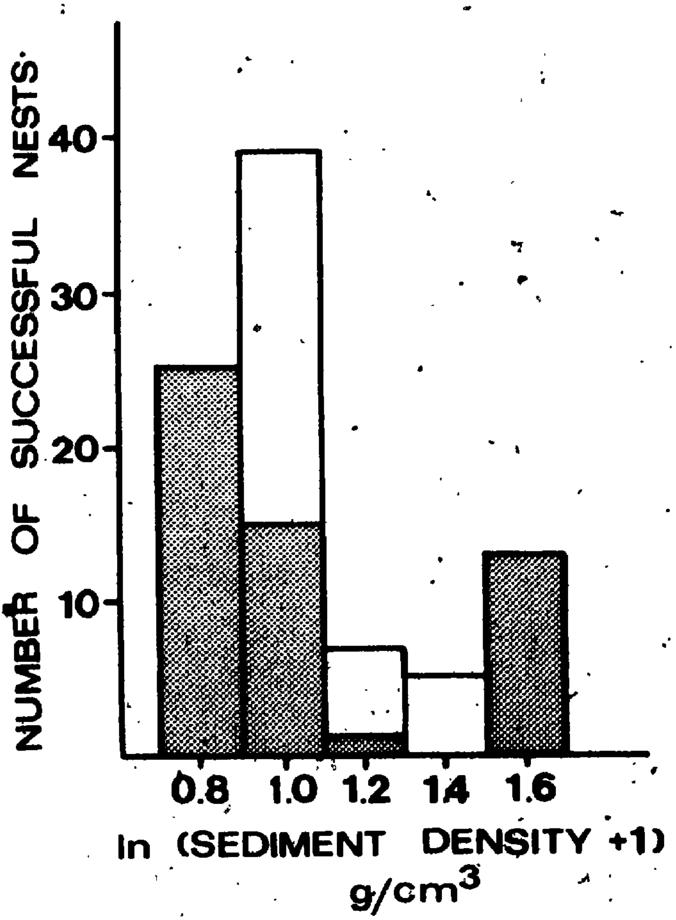
f.


NUMBER OF SUCCESSFUL NESTS
25
20
15
10
5
4.0
4.5
5.0
5.5
6.0
6.5
7.0
7.5
8.0
√NEST DIAMETER cm

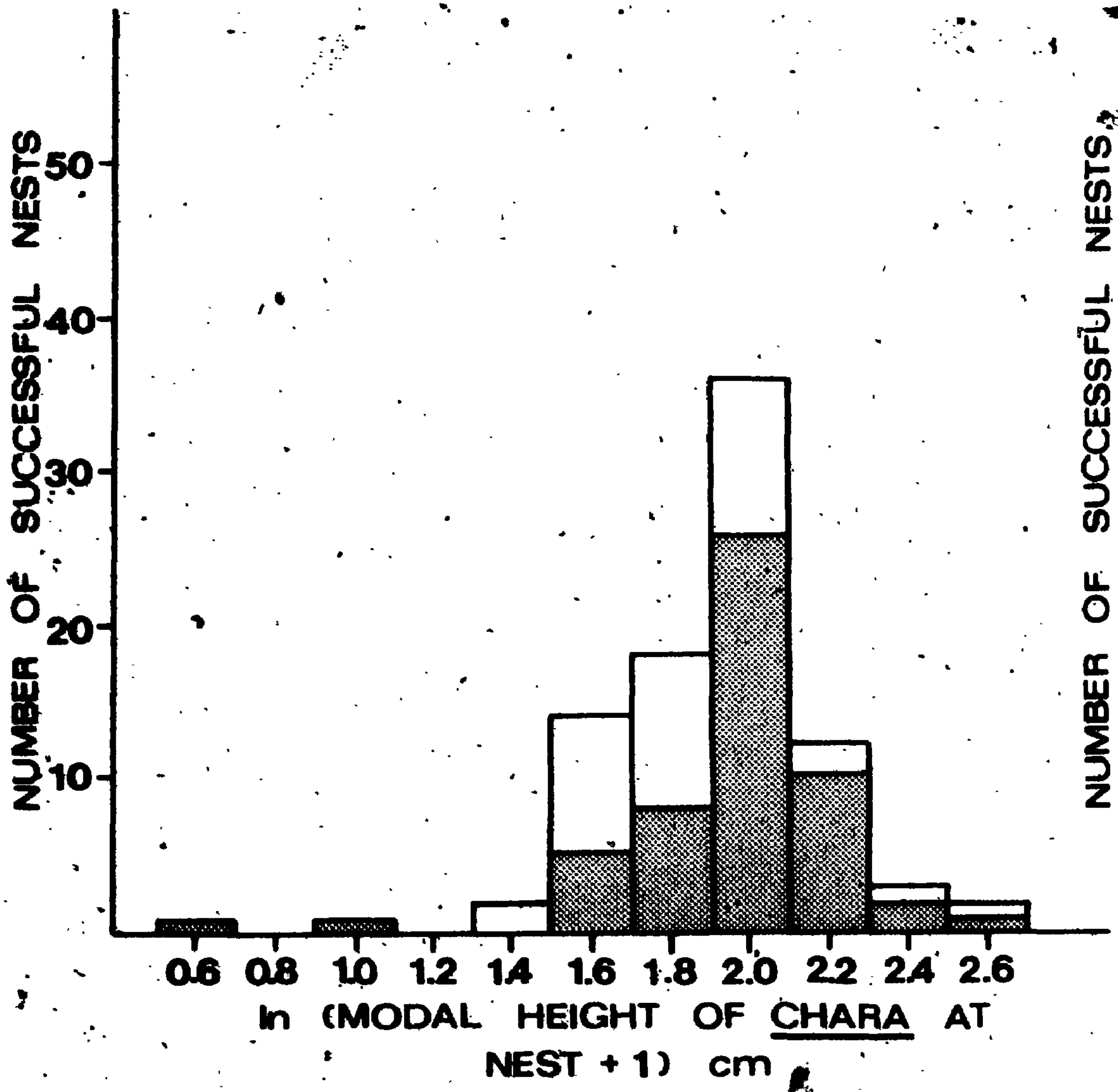
g.


NUMBER OF SUCCESSFUL NESTS
40
30
20
10
1
2
3
NEST MATERIAL

h.

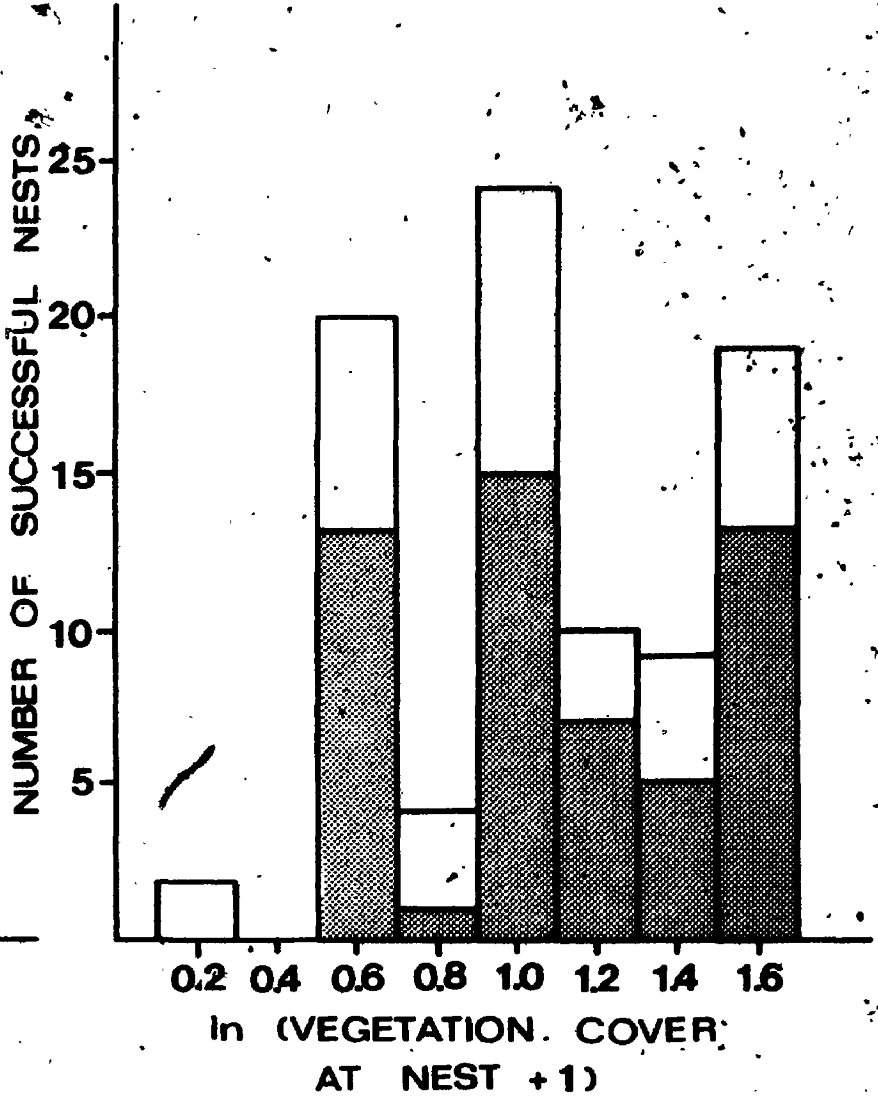

NUMBER OF SUCCESSFUL NESTS
40
30
20
10
0.8
1.0
1.2
1.4
1.6
ln (SEDIMENT DENSITY +1)
g/cm3

i.



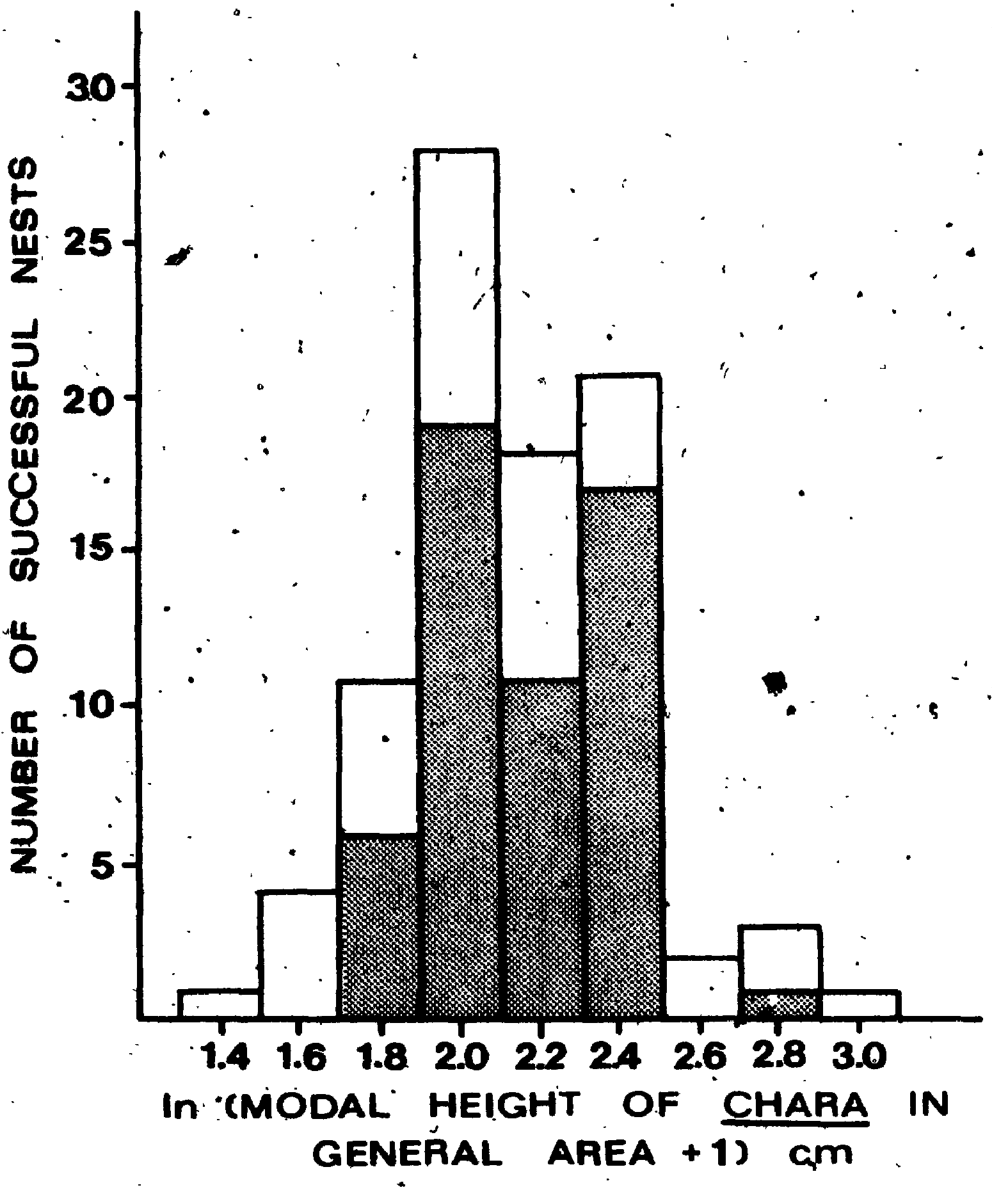
NUMBER OF SUCCESSFUL NESTS
10
20
30
40
50
0.6
0.8
1.0
1.2
1.4
1.6
1.8
2.0
2.2
2.4
2.6
ln (MODAL HEIGHT OF CHARA AT NEST + 1) cm

j.

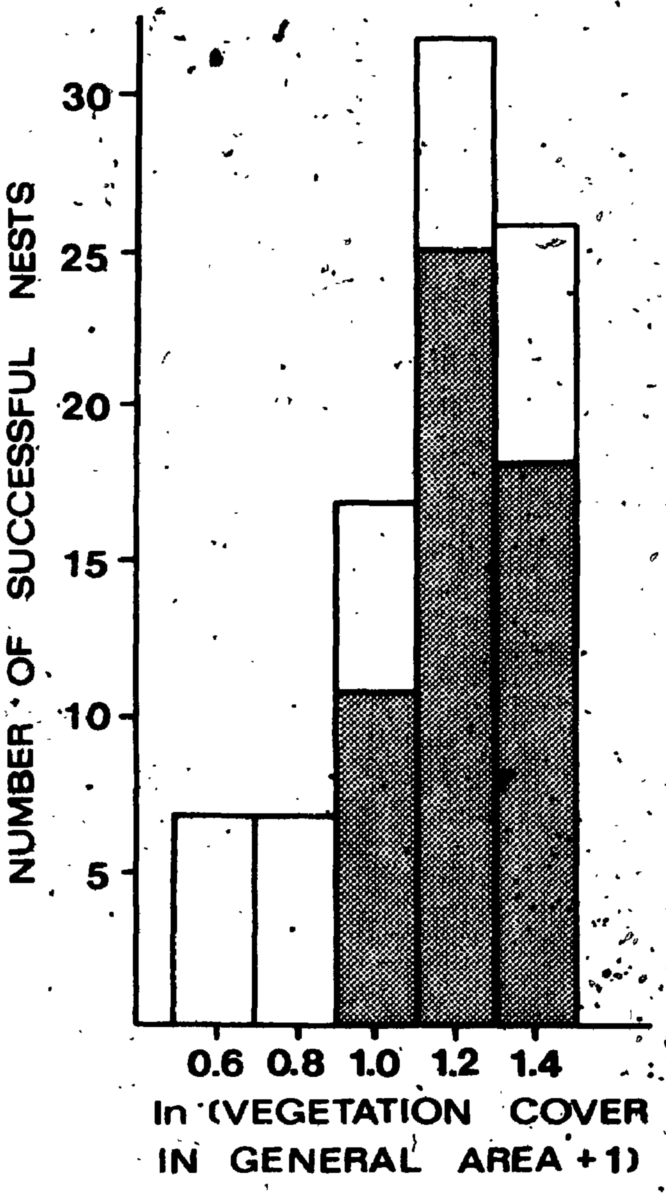


NUMBER OF SUCCESSFUL NESTS
5
10
15
20
25
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
ln (VEGETATION COVER AT NEST + 1)

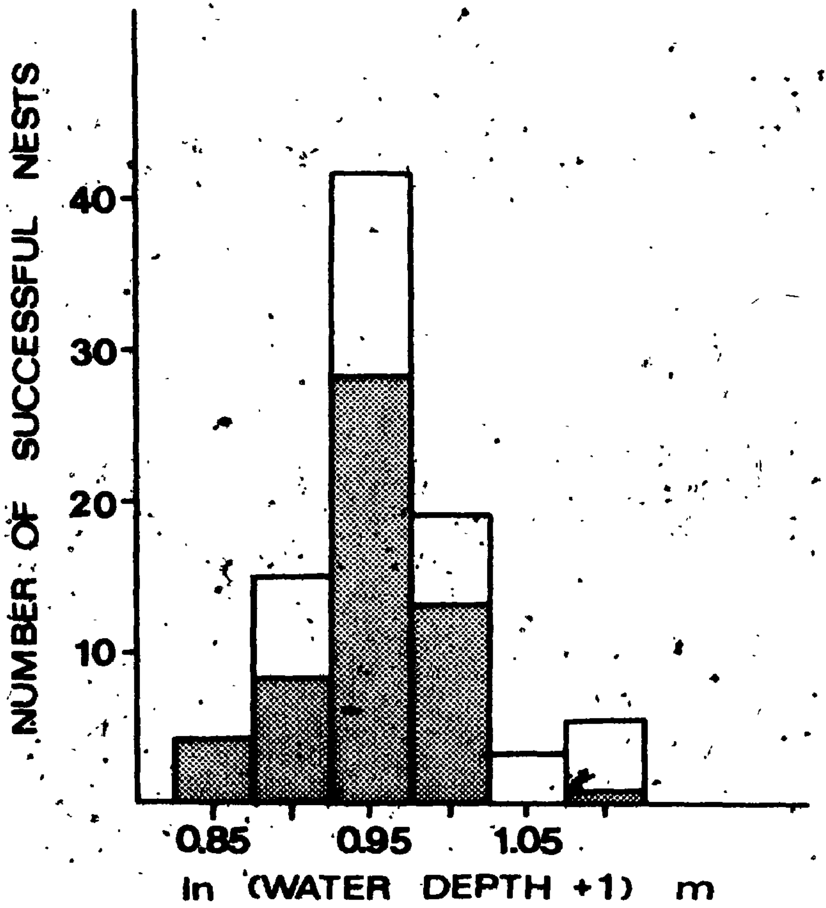
k.


NUMBER OF SUCCESSFUL NESTS
30
25
20
15
10
5
1.4
1.6
1.8
2.0
2.2
2.4
2.6
2.8
3.0
ln (MODAL HEIGHT OF CHARA IN GENERAL AREA +1) cm

l.

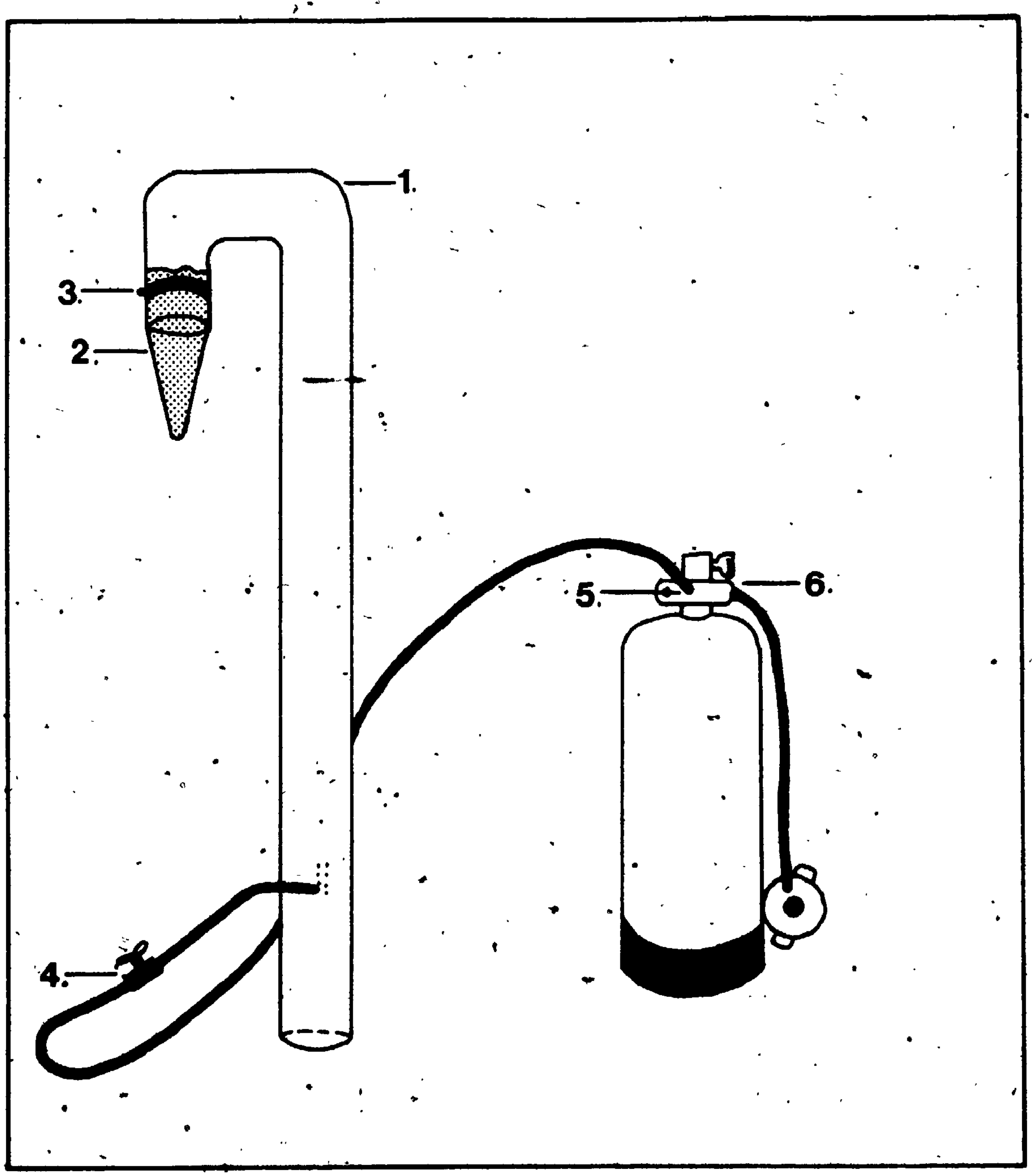

NUMBER OF SUCCESSFUL NESTS
30
25
20
15
10
5
0.6
0.8
1.0
1.2
1.4
ln (VEGETATION COVER IN GENERAL AREA +1)

m.


NUMBER OF SUCCESSFUL NESTS
40
30
20
10
0.85
0.95
1.05
ln (WATER DEPTH +1) m

APPENDIX 2

Diagram of underwater dredge used to collect "black-fry" from nests. 1. dredge 2. collection bay 3. band clamp 4. control valve 5. low pressure port 6. regulator


1.
3.
2.
5.
6.
4.

END

26 03 85

FIN