NAME OF AUTHOR/*NOM DE L'AUTEUR* BARRY CYRIL JONES

TITLE OF THESIS/*TITRE DE LA THÈSE* FEEDING, GROWTH, AND REPRODUCTION OF SPINY DOGFISH (SQUALUS ACANTHIAS L.) IN BRITISH COLUMBIA WATERS

UNIVERSITY/*UNIVERSITÉ* SIMON FRASER UNIVERSITY

DEGREE FOR WHICH THESIS WAS PRESENTED/*GRADE POUR LEQUEL CETTE THÈSE FUT PRÉSENTÉE* Ph.D.

YEAR THIS DEGREE CONFERRED/*ANNÉE D'OBTENTION DE CE GRADE* 1976

NAME OF SUPERVISOR/*NOM DU DIRECTEUR DE THÈSE* Dr. G. H. Geen

DATED/*DATÉ* April 30/76. SIGNED/*SIGNÉ*

PERMANENT ADDRESS/*RÉSIDENCE FIXE* [redacted]

FEEDING, GROWTH, AND REPRODUCTION
OF SPINY DOGFISH (SQUALUS ACANTHIAS L.)
IN BRITISH COLUMBIA WATERS

BY

Barry Cyril Jones

B.Sc., University of British Columbia, 1965
M.Sc., University of British Columbia, 1972

A DISSERTATION SUBMITTED IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY
in the Department
of
Biological Sciences

SIMON FRASER UNIVERSITY
April, 1976

APPROVAL

Name: Barry Cyril Jones

Degree: Doctor of Philosophy

Title of Thesis: Feeding, growth, and reproduction of spiny dogfish (Squalus acanthias L.) in British Columbia waters.

Examining Committee:

Chairman: J.S. Barlow

G.H. Geen, Senior Supervisor

R.M.F.S. Sadleir

E.B. Hartwick

K.S. Ketchen, Senior Research Scientist
Pacific Biological Station, Nanaimo, B.C.

N.J. Wilimovsky, External Examiner
Professor, University of British Columbia
Vancouver, B.C.

Date Approved: April 27, 1976

PARTIAL COPYRIGHT LICENSE

Title of Thesis/Dissertation:

FEEDING, GROWTH, AND REPRODUCTION OF SPINY DOGFISH (*SQUALUS ACANTHIAS* L.) IN BRITISH COLUMBIA WATERS

Author:

(signature)

BARRY C. JONES

(name)

April 30 /76.

(date)

ABSTRACT

Taxonomy, growth, reproduction, and feeding were studied in spiny dogfish (Squalus acanthias Linnaeus) of British Columbia waters.

Morphometric ratios, vertebral counts, and electrophoretic analyses of dogfish from east and west coasts of North America indicate that those in the northeastern Pacific Ocean comprise one of several discontinuous stocks of the cosmopolitan species, Squalus acanthias Linnaeus. Though the individual stocks exhibit statistically significant differences in meristic and biochemical characteristics, available data do not support subspecific status for any of the groups around the Americas.

Ages of dogfish in the Strait of Georgia have been estimated by an X-ray spectrometric technique which involves measuring variations in elemental composition within vertebrae. The results agree well with ages determined by counting dorsal spine circuli. Values of $K' = 0.070$, $L_{max} = 97.3$ cm, and $t_o = -4.5$ yr for males, and $K = 0.036$, $L_{max} = 128.5$ cm, and $t_o = -6.9$ yr for females are suggested for von Bertalanffy growth equations. First year growth, as determined by length-frequency analysis, is 5 cm for both sexes though growth in captivity is at least 50% greater.

Weight-length relationships were found to be $W(gm) = 0.17 \times 10^{-6} L^{3.47}(mm)$ and $W(gm) = 3.05 \times 10^{-6} L^{3.03}(mm)$ for full term and barren females respectively, and $W(gm) = 1.89 \times 10^{-6} L^{3.09}(mm)$ for males.

Lengths of dogfish when 50% of stock reach maturity are 78.5 and 93.5 cm for males and females respectively. At these lengths males are 19 yr of age and females are 29. Modal lengths of mature males and females are 85 and 100 cm respectively.

Mating occurs from October to January, with a peak in December. Males are capable of mating every year, with smaller dogfish mating earlier in the year than larger ones. Females mate every second year. Ovulation of 4 cm diameter eggs closely follows mating. The fertilized eggs are enclosed in gelatinous capsules for 4 months after which the embryos are released into the uterine cavity. The external yolk supply of the embryos is totally absorbed by parturition, although the internal yolk is not fully utilized until 2 months later. Parturition occurs from September to January, with a peak in November. Gestation is roughly 23 months. A mean of 7.14 progeny are produced per breeding female. Total mortality from parturition to modal length for mature females is 36%.

Data on stomach contents of 14,796 dogfish from British Columbia waters were used to construct a food budget, taking into consideration the seasonal rates of food consumption, and the relative biomass and metabolic requirements of different sizes and sexes. The major dietary components based on occurrence were 55% teleosts, 35% crustaceans, and 5% molluscs. The primary food items were herring (22%) and euphausids (14%). Prey was largely pelagic (80%), with fishes predominating in winter and invertebrates in summer. Fishes became more important in the diet with increasing size.

Experimental evidence indicated that dogfish consume twice as much food in summer as in winter. Estimates of annual consumption varied from five times stock weight for small dogfish to half that for larger animals. In terms of species of importance to commercial fisheries, preliminary analyses suggest that dogfish consume nearly 7 times the current annual catch of herring, but less than 0.1 times the catch of salmon.

DEDICATION

To the people for whom the dogfish
was more than just a nuisance,
but part of a way of life.

The Spiny Dogfish
of
British Columbia
Haida Indian art.
(after F. Boas, Primitive Art)

ACKNOWLEDGEMENTS

Sincere thanks are extended to Dr. G.H. Geen, my senior supervisor, who gave me the opportunity and support from his National Research Council grant to do this work, and diligently criticized the manuscript.

My thanks also go to the personnel of the Pacific Biological Station, Nanaimo, B.C., where the research was performed, and notably to Dr. K.S. Ketchen who made data and facilities available to me, and Mr. S.J. Westrheim who provided the use of personnel and equipment. Along with Dr. T.J. Mulligan who aided in the X-ray spectrometry, all three have provided invaluable comments on the manuscript.

Appreciation is also extended to E.J. Sandeman (Newfoundland), T. Jow (California), and J. Edgington (Alaska) for collection of specimens, and to the management of the former dogfish processing plant, Seafresh Pacific Products Ltd., of Chemainus, B.C., who who allowed me to take samples during 1973-74.

At Simon Fraser University credit is due to R. Ferguson, W. Thomson, K. Lee, R. Long, and M. Cheveldayoff for considerable technical assistance.

Assistance with the electrophoretic work was provided by Dr. H. Tsuyuki of the Vancouver Laboratory, Fisheries and Marine Service.

Thanks also go to Drs. N.J. Wilimovsky, R.M.F.S. Sadleir, F.J.F. Fisher, C.C. Lindsey, and E.B. Hartwick who reviewed all or parts of the manuscript.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

GENERAL INTRODUCTION

The spiny dogfish, Squalus acanthias L., is a species of small shark which is abundant in British Columbia waters. It is semi-pelagic in nature, inhabiting continental shelf regions. It is considered cosmopolitan in distribution though there is some debate as to whether the various stocks should be designated as subspecies.

In the past these dogfish have provided food and other useful materials for native Indians. During World War II an intensive fishery developed to provide a valuable source of vitamin A. The fishery collapsed due to overfishing (Barraclough 1948) and the development of synthetic vitamin A. The direct commercial importance of dogfish is now reduced to a small export food market, but they have a greater significance for their apparent effect on more lucrative fisheries by way of predation, gear destruction, and consequent loss of fishing time. Although some form of control of dogfish stocks seems desirable, few studies have attempted to determine those data required for proper management as recent literature reviews point out (Rae 1961; Alverson and Stansby 1963; Jensen 1966; Ketchen 1969).

To assess whether dogfish predation is significantly affecting the abundance of species of importance to commercial fisheries, adequate data on diet are necessary. Dogfish are considered opportunistic predators whose food consists chiefly of smaller fishes and various crustaceans. Though several studies provided data on diet (Razum 1952; Chatwin and Forrester 1953; Bonham 1954), no clear picture of their total feeding habits or impact on other species is available since data on consumption by different sizes and at certain times of the year are lacking. For this reason I did a feeding study.

Assuming management is forthcoming, an accurate time-growth function would be required. Growth in length has been estimated from tagging studies, dorsal spine circuli counts, length-frequency data, and other age determination methods (Bonham et al. 1949; Holland 1957; Ketchen 1975). Since no two studies produced the same results, age determination by a new method was attempted to clarify this issue.

To set up methods to regulate catch, the size distribution at sexual maturity and production of progeny in relation to recruitment to the fishery, and times of mating and breeding must be determined. Reproductively, dogfish are ovoviviparous and produce 6 to 7 pups during the winter months after a gestation period just short of two years (Bonham et al. 1949; Ketchen 1972). The actual times of mating and breeding were poorly delineated, and the size distribution of matures had not been determined. Though lengths at which 50% of stock reach maturity had been estimated, that for males had not been verified. To correct or verify these data, a study of reproduction was conducted.

In summary, the purpose of my work is to clarify some of the poorly understood aspects of dogfish biology indicated above to provide additional information for future management strategies. In this regard, research has been directed toward the four major areas of taxonomy, age and growth, reproduction and embryonic development, and food and feeding, each of which are presented as distinct chapters.

Chapter 1

TAXONOMIC RE-EVALUATION

INTRODUCTION

The spiny dogfish of northeastern Pacific waters ranges from Baja California to the southern Bering Sea, normally inhabiting the continental shelf regions (Springer and Garrick 1964, Hart 1973). Several authors (Bigelow and Schroeder 1948, Kato et al. 1967, Hart 1973) suggest this stock is a subspecies of the cosmopolitan species, Squalus acanthias Linnaeus, but lack evidence to that effect.

To clarify the taxonomic status of spiny dogfish in this area, I present data on morphometric ratios, vertebral counts, and electrophoretic characteristics from samples collected on east and west coasts of North America. These are compared with results of other workers on various stocks within the genus Squalus around the world.

MATERIALS AND METHODS

Spiny dogfish used in this study were collected during 1973-1974 on the west coast of North America, primarily from the Strait of Georgia, British Columbia. Other dogfish, predominantly larger individuals, were taken from Queen Charlotte Sound, B.C., and in Alaska, California, Newfoundland, and Nova Scotia waters.

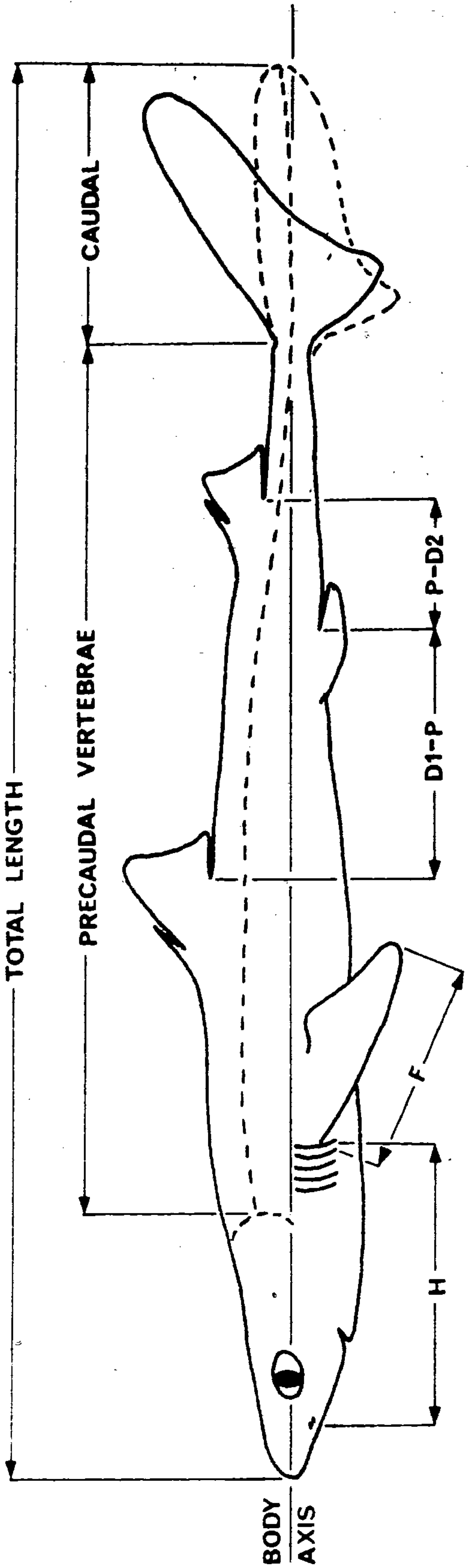
Morphometric ratios:

Strait of Georgia data were obtained from 182 individuals encompassing the full size range. Data were collected to permit calculation of two morphometric ratios. The first ratio (as used by previous authors) involves comparison of the length (F) of the pectoral fin measured from its origin at the fifth gill slit to its tip with head-length (H) as measured between the fifth gill slit and the center of the nares (Fig.1-1). The second ratio is the length (P-D2), in line with the body axis, from the rear base of the pelvic fin (P) to the rear base of the second dorsal fin (D2) compared with the length (D1-P) from P to the rear base of the first dorsal fin (D1). These ratios are related to total body length (tip of snout to tip of caudal fin when depressed to align with body axis) and sex of fish, following the method of Lindberg and Legeza (1956) and Forrester (1972).

Vertebral counts:

The number of vertebrae from 7 male dogfish ranging in length from 27 to 89 cm and 10 females from 27 to 109 cm collected from the Strait of Georgia were counted from X-ray negatives. Prior to X-raying a pin was placed at right angles to the body axis through the precaudal pit, a depression at the dorsal base of the caudal fin, to permit identification of precaudal and caudal vertebrae (Springer and Garrick 1964). Caudal vertebrae counts included the urostyle.

Fig. 1-1: Sketch of *Squalus acanthias* indicating the morphometric measurements used in this study (defined more fully in text).


TOTAL LENGTH
PRECAUDAL VERTEBRAE
CAUDAL
P-D2
D1-P
F
H
BODY
AXIS

Dogfish were X-rayed using the method and equipment described by Turner (1965). Vertebral columns were partially stripped of flesh for better resolution and placed over Kodak RP Royal 2 film at a distance of 1 m from a General Electric 15-90 X-ray unit.

Electrophoretic analyses:

Three or four adult dogfish of each sex from each area were frozen within 4 hr of capture. Muscle and blood samples were taken for starch gel electrophoresis from the recently thawed individuals and analysed following Tsuyuki et al. (1965).

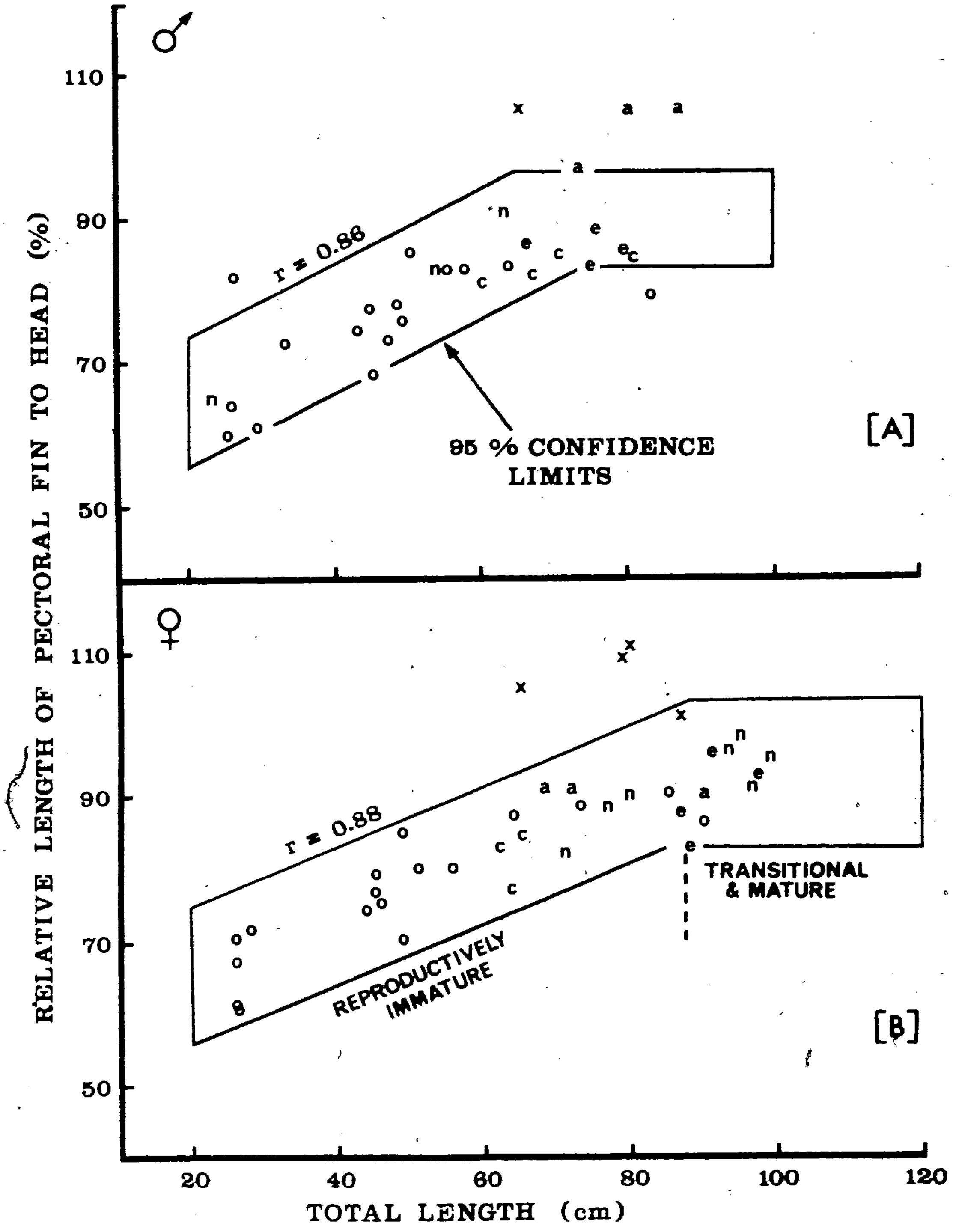
RESULTS

Data on relative length of the pectoral fin to head (F/H ratio) compared to body length for dogfish in British Columbia waters are presented in Table 1-1. Lengths and F/H ratios for immature dogfish from the Strait of Georgia (Fig.1-2) are positively correlated ($P<0.05$), but the data from those showing some sign of gonad or secondary sexual characteristic development (transitional dogfish) and mature animals are not. These data are not plotted, but enclosed areas representing the 95% confidence limits around the data over the length range sampled are indicated (Fig.1-2). This permits a more ready comparison of dogfish data from other locations and stocks.

Table 1-1: Comparison of pectoral fin length relative to head (F/H ratio) for <u>Squalus</u> <u>acanthias</u> from British Columbia waters.

Area/Source/Sex	Number Sampled	Data Range	
		Length (cm)	Ratio (%)
<u>Strait of Georgia</u>			
This study:			
Males (immature)	46	25.3 - 69.4	57.1 - 91.5
(trans. & mature)	27	71.8 - 97.8	84.4 - 97.2
Females (immature)	68	24.3 - 94.5	54.2 - 98.6
(trans. & mature)	32	78.3 - 122.5	80.6 - 104.3
Forrester (1972):			
Males	168	71.6 - 91.5	81.8 - 100.0
Females	33	72.6 - 113.5	85.2 - 100.0
<u>Queen Charlotte Sound</u>			
Forrester (1972):			
Males	51	48.0 - 89.8	73.9 - 97.8
Females	51	47.6 - 111.7	74.8 - 95.7

Fig. 1-2: Relationship of relative length of pectoral fin to head (F/H) and total body length for <u>Squalus acanthias</u> (A) males and (B) females. Enclosed areas represent the 95% confidence limits around the Strait of Georgia data (not plotted) for the length ranges sampled. Regression equations of this ratio on length of immature animals are $R(\%) = 54.4 + 0.506\ L(\mathrm{cm})$ for males and $R(\%) = 57.2 + 0.409\ L(\mathrm{cm})$ for females ($P < .05$). Regressions were not significant for transitional (see text) and mature dogfish; means ± 1 SD are 89.7 ± 3.4 and 92.6 ± 5.1 for males and females respectively. Data from Lindberg and Legeza (1956) for the short fin (o) and long fin (x) forms are superimposed, as are those of Garrick (1960) for New Zealand (n) and dogfish in this study from the east coast of Canada (e), Alaska (a), and California (c).


♂
110
90
70
50
r = 0.86
95 % CONFIDENCE LIMITS
[A]
♀
110
90
70
50
r = 0.88
REPRODUCTIVELY IMMATURE
TRANSITIONAL & MATURE
[B]
20
40
60
80
100
120
TOTAL LENGTH (cm)
RELATIVE LENGTH OF PECTORAL FIN TO HEAD (%)

Data on the relative position of the pelvic fin to the dorsal fins (P-D2/D1-P ratio) compared to body length for the various species groups within the genus Squalus from this and other studies are given in Table 1-2. For Strait of Georgia dogfish (Fig.1-3) this ratio is negatively correlated ($P<0.05$) with length.

Dogfish vertebral numbers determined from North American east and west coast specimens are presented in Table 1-3. Neither total length nor sex are correlated with vertebral numbers.

Electropherograms of muscle myogens and blood hemoglobins for North American east and west coast dogfish are illustrated in Fig.1-4. Fish of different sizes and both sexes from the same area yielded similar results.

DISCUSSION

The spiny dogfish type specimen, designated as Squalus acanthias by Linnaeus, was described from European waters in 1758. Since that time various stocks of morphologically similar animals in different parts of the world have been referred to by this name, although sometimes as subspecies, or even different species. Many authors consider the northeastern Pacific stock as belonging to this species, but further propose that it be accorded subspecific rank based on differences in F/H ratio and vertebral numbers.

Table 1-2: Comparison of the position of the pelvic fins relative to the dorsals (P-D2/D1-P ratio) for the species group divisions within the genus *Squalus*.

Group/Source/Sex	Number Sampled	Data Range Length (cm)	Data Range Ratio (%)
acanthias:			
This study - males	80	25.3 - 97.8	92.1 - 54.8
- females	102	24.3 - 122.5	78.7 - 45.6
Bigelow and Schroeder (1957)	-	-	≥100
Garrick (1960)[a]	8	23 - 99	293 - 80
blainvillii:[b]			
Bigelow and Schroeder (1957)	-	-	<100
Garrick (1960)[a]	6	21 - 98	327 - 152
megalops-*cubensis*:			
Lindberg and Legeza (1956)[c]	-	-	126
Bigelow and Schroeder (1957)	-	-	>100

---

[a] Data derived from Fig.2, p.523.

[b] *blainvillii* (Garrick 1960) = *fernandinus* (Bigelow and Schroeder 1957).

[c] Their *S. brevirostris* = *S. megalops* (Garrick 1960); mean value only given.

Fig. 1-3.: Relationship of relative position of pelvic fins to dorsal fins (P-D2/D1-P) and total body length for <u>Squalus</u> <u>acanthias</u> (A) males and (B) females. Enclosed areas represent the 95% confidence limits around the Strait of Georgia data (not plotted) for the length ranges sampled. Regression equations of ratio on length are $R(\%) = 77.4 - 0.102\ L(cm)$ for males and $R(\%) = 73.3 - 0.145\ L(cm)$ for females ($P<.05$). Data from Lindberg and Legeza (1956) for the short fin (o) and the long fin (x) forms are superimposed, as are those of this study for the east coast of Canada (e), Alaska (a) and California (c).

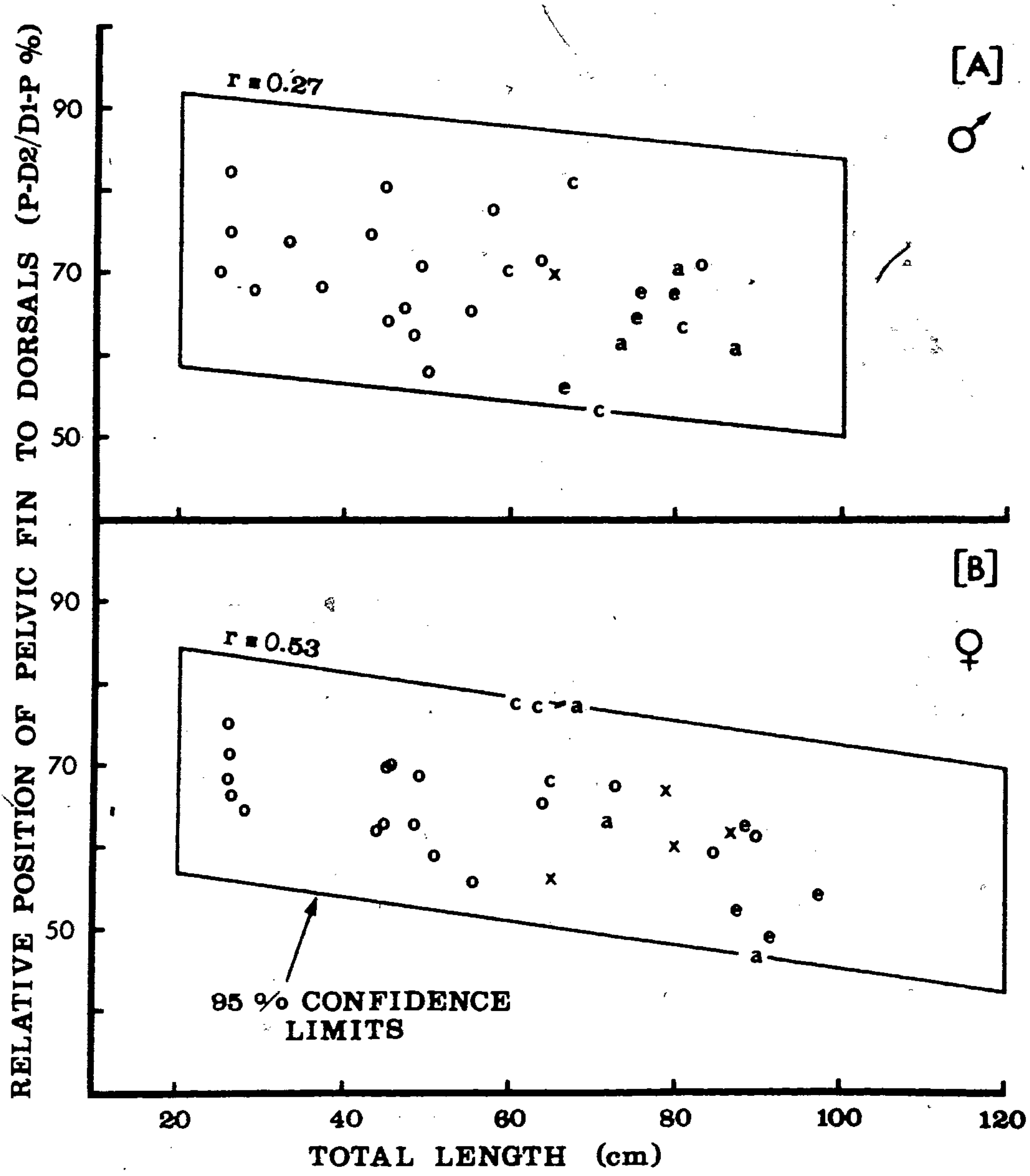

[A]
♂
r = 0.27
[B]
♀
r = 0.53
95 % CONFIDENCE LIMITS
RELATIVE POSITION OF PELVIC FIN TO DORSALS (P-D2/D1-P %)
TOTAL LENGTH (cm)
90
70
50
20
40
60
80
100
120
o
c
x
a
e

Table 1-3: Comparison of vertebral numbers of *Squalus acanthias* from the east and west coasts of North America.

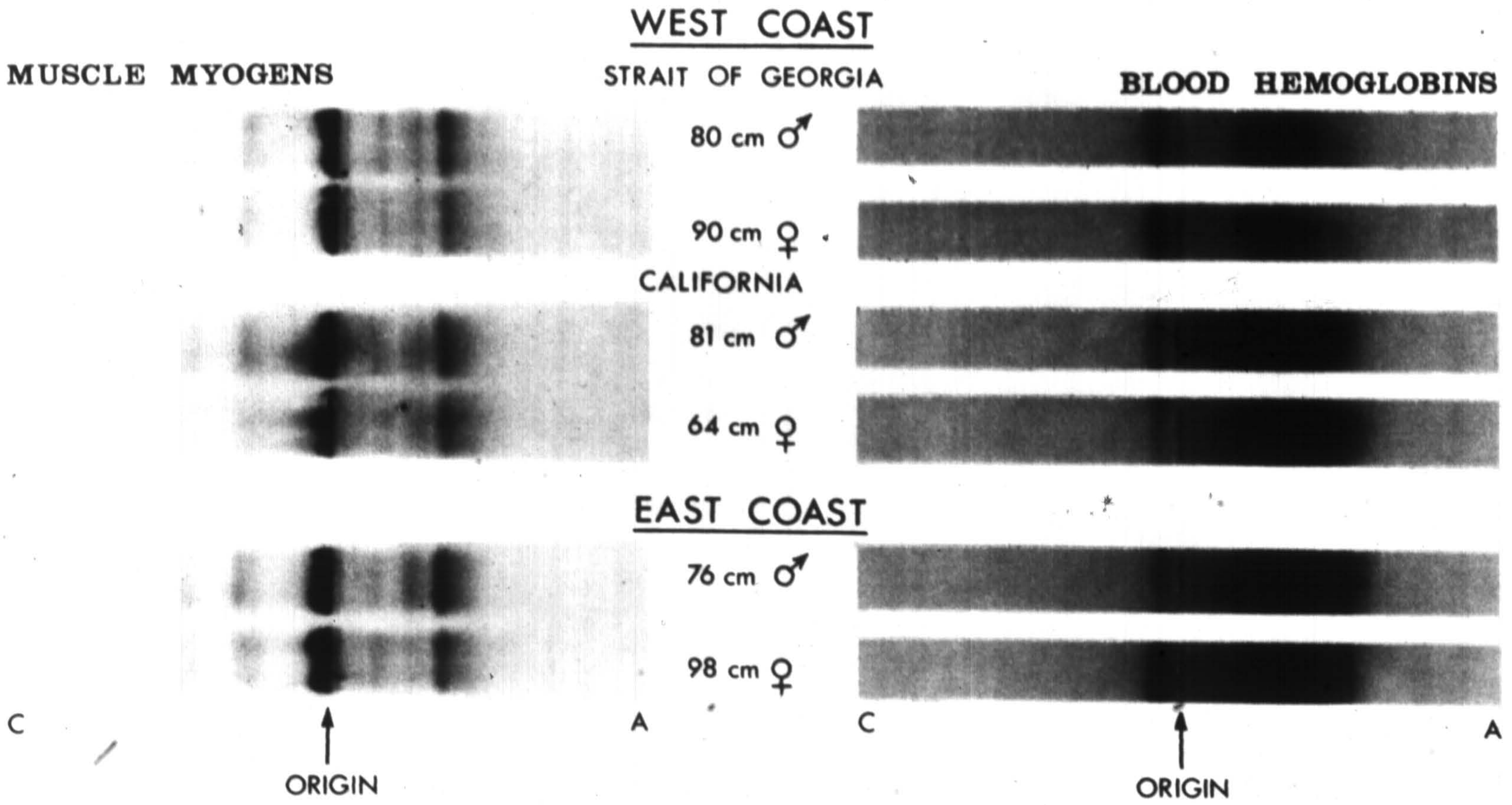
Area	Number sampled	Mean number of vertebrae Precaudal	Caudal	Total	Range of total
Alaska	6	71.5	28.0	99.5	96-104
British Columbia					
a) Queen Charlotte Sound	3	71.5	28.5	100.0	98-103
b) Strait of Georgia	17	71.0	29.1	100.1	97-103
California	7	72.6	28.1	100.7	97-109
West Coast[a]	33	71.5±2.1[b]	28.6±1.0	100.1±2.7	96-109
East Coast	8	82.7±1.8	30.2±1.4	112.9±2.4	109-116
Difference		11.2[c]	1.6	12.8[c]	

[a] Mean of all west coast data presented above.

[b] One standard deviation.

[c] Difference between west and east coast significant at 95% confidence level.

Fig. 1-4: Comparison of electropherograms of muscle myogens and blood hemoglobins for *Squalus acanthias* from the east and west coasts of North America. Solutions were introduced at the origins. C = cathode and A = anode.

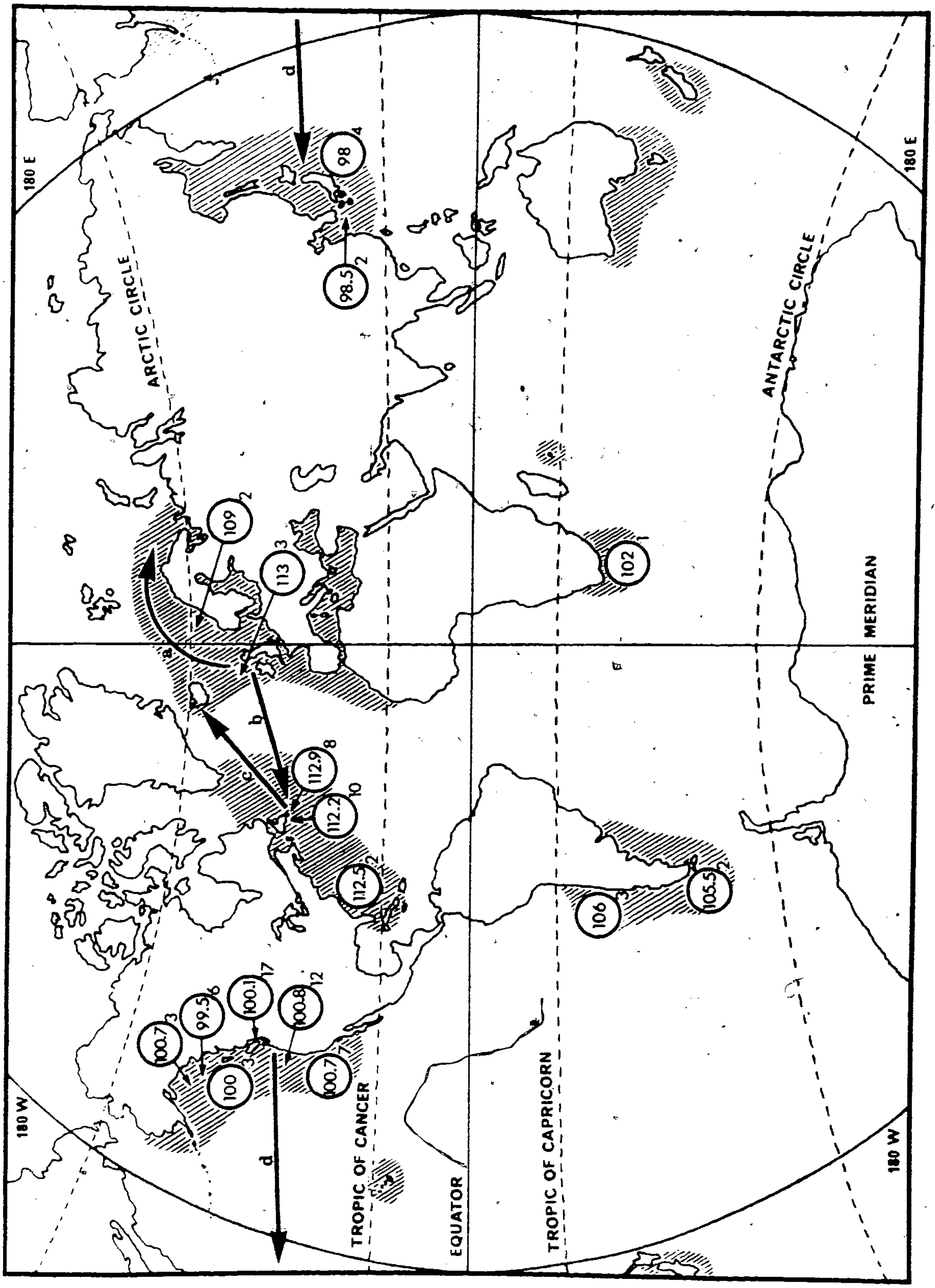

MUSCLE MYOGENS
WEST COAST
STRAIT OF GEORGIA
BLOOD HEMOGLOBINS
80 cm ♂
90 cm ♀
CALIFORNIA
81 cm ♂
64 cm ♀
EAST COAST
76 cm ♂
98 cm ♀
C
A
C
A
ORIGIN
ORIGIN

Lindberg and Legeza (1959) suggested that spiny dogfish on the east and west coasts of North America be called S.a. acanthias and S.a. suckleyi respectively, based on F/H ratio differences. My F/H ratio data for the Strait of Georgia indicate significant positive regressions on length for reproductively immature animals, but not for transitional and mature ones. Most of my other ratio data from Alaska, California, Newfoundland, and Nova Scotia dogfish fall within the Strait of Georgia F/H data confidence limits (Fig. 1-2), as do those of Garrick (1960) for New Zealand dogfish and those of Lindberg and Legeza (1956) for their short fin form from European and northwestern Pacific waters. This suggests that there is no justifiable subspecific distinction among dogfish from these areas. However, the F/H ratio of the long fin form (Lindberg and Legeza 1956) as represented by specimens from the Barents and White Seas in northern U.S.S.R. waters and off California, generally falls outside the Strait of Georgia confidence limits. The California long fin data are questionable, being derived from one 65 cm male preserved for nearly 100 yr. While most of my dogfish were measured in the freshly killed state, the Alaska ones were preserved in formalin first, and had F/H ratios for males similar to those found by Lindberg and Legeza (1956). Two 60 cm Strait of Georgia males preserved for 10 days in isotonic 10% formalin solution exhibited a 2.1% increase in F/H ratio due to differential shrinkage, and a 5.1% length decrease. Thus, shrinkage of head and body both tend to produce a greater F/H ratio.

Accordingly, it appears that the long fin status of the single male described by Lindberg and Legeza (1956) is likely an artifact of preservation. The data collected from males of all stocks sampled in this and other studies appear likely to fall within the Strait of Georgia confidence limits.

The long fin data of Lindberg and Legeza (1956) for female dogfish from northern U.S.S.R. waters were taken from four individuals of 65 to 87 cm length. The F/H ratios of three fall outside my Strait of Georgia confidence limits (Fig.1-2), and one of these is near the upper extremity of my range for females (Table 1-1). Since the long fin ratios are greater than those from the preserved Alaska females, preservation effects do not appear to account for the F/H ratio differences. However, when relative fin lengths of dogfish from around the world are compared to the mean summer sea surface temperatures at their locations of capture, a negative regression is obtained ($r=-0.78$, $p<0.001$, $n=18$). This indicates that the F/H ratio is environmentally influenced which suggests that subspecific distinction for the long fin forms is not justified. In addition, dogfish migrations have occurred between regions designated by Lindberg and Legeza (1959) as having the long and short fin stocks (Fig.1-5). Interbreeding would tend to eliminate fin differences even if this were a purely genetic character. Thus, variations in F/H ratio do not appear to indicate the existence of differences between stocks that are not attributable to preservation artifacts or environmental modifications.

Fig. 1-5: Global distribution of <u>Squalus acanthias</u> (shaded area) as derived from Bigelow and Schroeder (1957), Lindberg and Legeza (1956), Springer and Garrick (1964) and Hart (1973) showing mean total vertebral numbers (circled) and the number of dogfish sampled to lower right (from Templeman 1944, Springer and Garrick 1964, this study) for different areas. Arrows indicate apparent movements of dogfish between stocks as determined by tagging studies: a = Scotland to Barents Sea (Aasen 1962), b = Scotland to Newfoundland (Holden 1967), c = Newfoundland to Iceland (Templeman 1958), and d = Washington to Japan (Anonymous 1952).


180 W
180 E
180 W
180 E
ARCTIC CIRCLE
TROPIC OF CANCER
EQUATOR
TROPIC OF CAPRICORN
ANTARCTIC CIRCLE
PRIME MERIDIAN
d
d
b
c
100.7 3
99.5 6
100.1 17
100.8 12
100 3
100.7 7
112.5 2
112.2 10
112.9 8
113 3
109 2
102 1
106 3
105.5 2
98.5 2
98 4

The other characteristic proposed to distinguish the northeastern Pacific dogfish as a subspecies of Squalus acanthias distinct from the Atantic form was vertebral numbers. My data from east and west coasts of North America indicate that total vertebral numbers are significantly different (Table 1-3). However, a southeastern Pacific stock has vertebral numbers intermediate to these groups (Fig. 1-5). Mayr (1969) points out that if the data ranges for particular species characteristics overlap between supposedly discontinuous stocks by more than 20%, then by convention they do not deserve subspecific recognition. Overlap exceeds 20% between the northeastern Pacific and southeastern Pacific stocks, and also between this latter stock and the northwestern Atlantic stock (Table 1-4). Thus, subspecific designation for the northeastern Pacific dogfish relative to the Atlantic form on the basis of vertebral numbers is not appropriate.

To further examine the possibility of subspecific distinction between dogfish from east and west coasts of North America, muscle myogens and blood hemoglobins were electrophoretically analysed. Close similarity of muscle myogen patterns (Fig. 1-4) indicate that on a geological time scale these stocks have only recently become separated, or that some genetic interchange still occurs between them. However, a comparison of blood hemoglobins, which may be more readily adaptable than muscle myogens (Tsuyuki et al. 1965), indicate a difference between the dogfish stocks from the Strait of Georgia and

Table 1-4: Vertebral numbers of *Squalus acanthias* stocks around North and South America showing calculated degree of differentiation between adjacent stocks.[a]

Stocks	Number Sampled	Total vertebral number		CD[b]	Overlap (%)
		Mean	1 SD		
East Coast N.A.	20	112.5	2.70		
				1.27	21
S. South America	5	105.8	2.59		
				1.05	29
West Coast N.A.	47	100.3	2.67		

[a] Combined data of this study, Springer and Garrick (1964), and Templeman (1944).

[b] CD (coefficient of difference) = (mean 1 - mean 2)/(SD 1 + SD 2) where mean 1 is the largest (Mayr 1969). Conventional level of subspecific differentiation is 1.28 or greater (20% overlap or less of stock characteristic).

the east coast of North America, with the pattern of the California animals somewhat intermediate. These differences are not attributable to variations between fetal and adult hemoglobins (Manwell 1963), as the dogfish I used are generally of the same size. A gradual change in blood hemoglobins from the northeastern Pacific to the southeastern Pacific to the north Atlantic is thus indicated, but the apparent continuity of this change removes any support for subspecific designation of regional stocks. Considering the distribution of *Squalus acanthias* (Fig.1-5) and the movements of tagged animals between stocks, dogfish from any of these areas are likely to be little different.

Additional evidence against subspecific distinction of dogfish stocks is obtained from the P-D2/D1-P ratio, which, in my data, has a negative regression on length (Fig.1-3). Thus, P-D2/D1-P ratio data collected from all areas fall within the 95% confidence limits of the Strait of Georgia data. Though the P-D2/D1-P ratio has contributed to the clarification of the subspecific question for the northeastern Pacific stock of *Squalus acanthias*, it has also been the source of some confusion in the literature when applied to the separation of species groups within the genus *Squalus*.

Recent authors (Bigelow and Schroeder 1957, Garrick 1960) have classified all forms of *Squalus* under one of three major species groups as follows: (1) acanthias, (2) blainvillii (fernandinus), and (3) megalops-cubensis. The northeastern Pacific dogfish is placed in the first group based on shape of pectoral fins, position of first dorsal fin relative to pectorals, appearance of external nares, color pattern, and the position of the pelvic fins relative to the dorsals (P-D2/D1-P ratio). With regard to this latter characteristic as a means of separating species groups, my data (Fig. 1-3) indicate that the pelvic fins are closer to the second dorsal, are relatively closer in larger individuals, and are approximately 8% closer for females than males. Similar data from other northeastern Pacific dogfish stocks fall within the 95% confidence limits of my data, as do those from the east coast of North America. However, for acanthias dogfish, Bigelow and Schroeder (1957) and Garrick (1960) reported the pelvic fins were closer to the first dorsal (Table 1-2). For the blainvillii group these two authors differ by noting the pelvic position as on opposite sides of the midpoint between the dorsals. In the megalops-cubensis group Bigelow and Schroeder (1957) and Lindberg and Legeza (1956) noted that the pelvics were closer to the first dorsal than the second. Garrick (1960) confirmed this observation by reporting no difference in pelvic fin position between this group and the blainvillii group in which the pelvics were also closer to the first dorsal. My data (Fig. 1-3) suggest that the ratio differences reported by these workers may have resulted from the effects of length and sex. Although the species groups may be separable in other ways, it appears that the P-D2/D1-P ratio substantially overlaps among groups and is therefore of little use in distinguishing species, although its value might be enhanced if supplemented with data on length and sex.

In summary, the value of the morphometric ratios, F/H and P-D2/D1-P, used by other authors to distinguish between subspecies and species groups respectively, is open to doubt. However, dogfish migration and muscle myogen patterns indicate that the northeastern Pacific Ocean spiny dogfish is one of several stocks comprising the cosmopolitan species, *Squalus acanthias*. Though the North American east and west coast stocks of dogfish show differences in vertebral numbers and blood hemoglobin patterns, conventional analyses fail to justify subspecific status as a result of overlapping characteristics between these groups and a South American stock which has intermediate characteristics. Thus, maintenance of the present taxonomic status of *Squalus acanthias* (Linnaeus) indicated by the American Fisheries Society (Bailey et al. 1970) for the northeastern Pacific dogfish is supported.

Chapter 2

AGE AND GROWTH

INTRODUCTION

The age of many fishes can be determined by examining scales, otoliths, or bones for evidence of seasonal changes in deposition of hard tissue. However, most of these methods are not applicable to the elasmobranchs. In this study I attempted to determine ages for the spiny dogfish using X-ray spectrometry and have related the data thus obtained to changes in length and weight. This particular species is readily available in British Columbia waters, and is among the few living elasmobranchs with dorsal spines. These spines were previously used in an earlier ageing study employing circuli counts. The results obtained with that method were compared with those obtained by X-ray spectrometry. Length-frequency data and growth of young in captivity also provided some data for independent estimates of age.

The possibility of age determination by X-ray spectrometry was suggested by Calaprice et al. (1971) who noted differences in elemental composition between those portions of molluscan shells laid down in summer and winter. In the hard tissue of many fishes it is possible to observe such annual variations in deposition visually with relatively low power magnification. In dogfish, except for dorsal spines, no visual patterns reflecting seasonal changes in growth were evident in hard tissue. However, it is possible that as environmental conditions change seasonally, the metabolic uptake of different elements may also change, either as a function of biological activity or element availability. Food consumption or availability might limit the uptake of a particular element or environmental factors may differentially affect uptake of elements from water. X-ray spectrometric measurement of such quantitative differences in seasonal deposition of elements may offer a new method of age determination.

MATERIALS AND METHODS

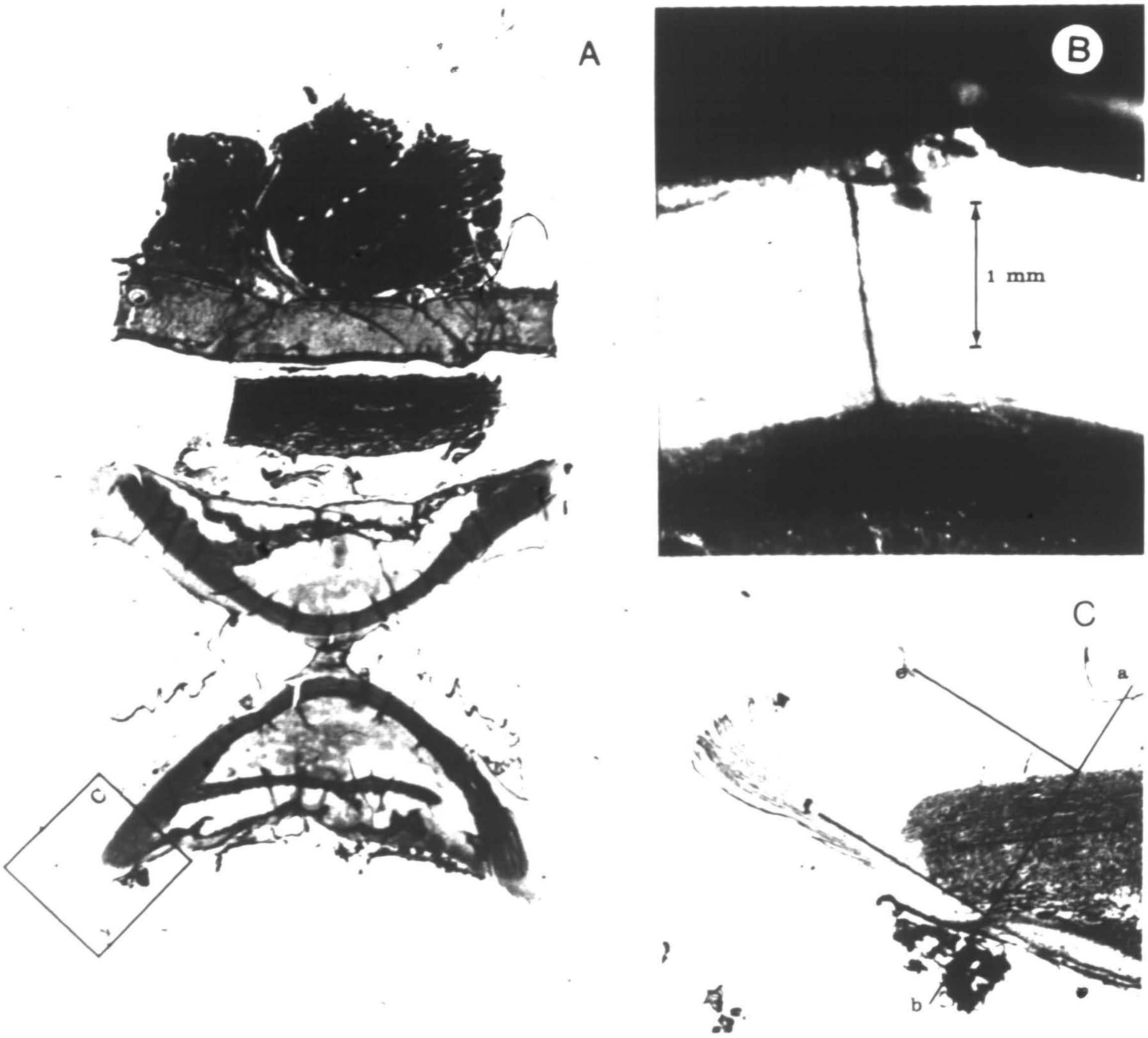
X-ray spectrometry:

The 7 male and 8 female dogfish used in this study were collected between May, 1974, and February, 1975, from the Strait of Georgia off Nanaimo, B.C., Canada. One individual from each 10 cm span over the normal length range for each sex was used.

The hard tissue of the spiny dogfish suitable for X-ray spectrometric age analysis is limited to the skeleton, lenses, and dorsal spines. The choice of structure used is governed by its mode of formation and ease of preparation. Spines were not used because their formation results in a structure analogous to a series of nesting cups, a cross-section of which might not cut through all layers at any one place (Holden and Meadows 1962). Though the lenses show definite concentric form in cross-section, their preparation is difficult as they are too soft in the fresh state and too hard and subject to irregular fracturing in the frozen or fixed state. In some fixatives they are relatively easy to section, but the chemical composition is radically altered by fixation. Much of the skeleton is also unsuitable as it is primarily cartilage and is drastically misshapen when freeze-dried, a necessary prerequisite for electron microscopy. However, vertebrae contain inorganic material (largely calcium and phosphorus) embedded in the cartilage and exhibit an increased percentage ash content with increased size (Doyle 1968), thus suggesting a direct relationship to age. Since they also have the thickest embedded areas (Benzer 1944) which allows easier X-ray analysis, they seemed an obvious choice for this work.

Vertebrae were selected from the region where they are the largest, immediately anterior to the first dorsal fin. Excess tissue was removed, the vertebrae separated, and frozen. Though I used only frozen material, twenty-four hours fixation in alcohol had no demonstrable effect on elemental composition. However, preservation in formalin or Bouin's solution eroded the embedded area and reduced the measured age. Subsequent preparation involved freeze-drying the vertebrae for 24 hr and shaving one end with a razor blade to remove the intervertebral cartilage. A stained sagittal section through the embedded area thus exposed (Fig. 2-1A,C) indicated that this procedure transected all the tissue layers in this region. The vertebrae were then glued (Lepage's Bondfast) to aluminum sample stubs and coated with a micro-layer (approx. 50Å) of carbon to minimize the

Fig. 2-1: Dogfish vertebrae used for X-ray spectrometry in (A) sagittal section indicating embedded area (stained), (B) cross-section showing scan range (dark line caused by electron beam), and (C) tissue orientation. ab = cut for sample preparation of whole vertebra, cd = direction of tissue fibres in embedded area, and ef = scan range.


A
B
1 mm
C
C
a
b

possible effects of surface charging which could deflect the electron beam or reduce repeatability. The sample showed no evidence of contamination from the glue.

The equipment used in elemental analysis consisted of an ETEC Autoscan scanning electron microscope, a Nuclear Semi-conductor lithium-drifted silicon detector, and a Northern Scientific Econ II pulse height analyser. This is an energy-dispersive X-ray spectrometric system in which electrons striking the sample produce X-rays, some of which pass through a collimator to the detector. The pulse thus generated is relayed through amplifiers to the analyser which has a series of memory units (channels) that divide the spectrum under consideration into equal energy intervals. The energy level of the X-rays produced by each element differs; higher emission energies result from elements with higher atomic weights. The more abundant elements appear as peaks above a background radiation level in a particular channel range on the cathode ray tube display of the analyser. The integrated area under each peak is determined by summation of individual channel data, and can be read from an additional visual display. Further details on the theory and operation of this type of system are presented by Woldsetn (1973).

In this work a collimator with a 1 mm diameter aperture was used. A larger aperture decreased sensitivity by allowing the passage of more background X-rays, and a smaller one decreased the count rate, thereby increasing analysis time. The collimator was fixed at approximately 70° off the vertical electron beam. Best results were obtained when the sample was preferentially inclined towards the collimator at 45° off vertical. For excitation purposes an accelerating voltage of 30 Kv with a beam current of approximately 1.0 x 10^{-9} amps yielded highest optimum X-ray production. To maximize count rate and thus minimize analysis time, the sample position was adjusted on its three-dimensional axis with reference to feedback impulses from the analyser such that the excitation area was in line with the collimator.

In my samples calcium and phosphorus were selected for analysis. The energy spectrum within which elements could be analysed with this system encompassed approximately 30 elements bounded by sodium at the lower level and molybdenum (near beam energy) at the higher level. Silicon and aluminum could not be used reliably as they form part of the detector construction materials. The ability of specific types of equipment to reliably analyse different elements is further discussed by Rhodes (1966).

The sample was rotated to align the desired part of the scan range (embedded area) with the horizontal stage axis most nearly perpendicular to the sample-collimator direction. This was necessary as the sample tilt was on the latter axis, and moving it resulted in the electron beam striking the sample at a different vertical position. Preliminary analysis resulted in distinct peaks with an analysis time of 100 seconds per area. Integration gates were set around each peak at background level so that the corrected number of counts under their curves could be determined by subtracting the mean background from the total between the gates. A $CaHPO_4$ standard verified that calcium and phosphorus peaks were correctly identified. Tests did not indicate any appreciable effects of sample topography, alteration of composition during analysis, vacuum system contamination, or differential absorption of X-rays among elements, any one of which could have affected the analyses.

Analysis was begun with low magnification at the outer edge of the scan range, where any changes in elemental patterns might be closer together reflecting slower growth with increasing age. The range was traversed (Fig.2-1B) with non-overlapping sequential areas. If no cycles were evident after the first series, the micrometer increment was reduced and the magnification increased to allow more analysis areas within the scan range. This process was repeated until cycles were detected and only verified by further increases in magnification.

Following the scan, the corrected data were plotted and the number of peaks were counted and used as an index of age. The validity of observed peaks was established by reference to the possible range of equipment counting error. Beam current drift at the sample level was generally slow (0.01×10^{-9} amps per minute) and unidirectional, and thus had little effect on area counts over the short time intervals required to delineate adjacent peaks and troughs in this study. Possibly the general increase in element peak height from periphery to core as seen in Fig.2-3 resulted from current drift. Using a brass standard, instrument variability at the count level used in this study produced a reading error of ±0.9% on copper and zinc (95% confidence limits) on the corrected count level for the first 500 seconds. As error increased with decreased counts, an additional method of error computation was employed in which 95% confidence limits were $A \pm 1.96\sqrt{TA}$, where A was the corrected count for the element and TA was the uncorrected count. In any single analysis, the largest of these error calculations was used in evaluating peak-trough differences. I assumed that differences had to exceed twice the error at the 95% confidence limit level to be considered valid.

Length-frequency analysis:

The data used in the length-frequency analysis consisted of my records plus those collected by the Pacific Biological Station, Nanaimo, B.C., from the Strait of Georgia over the past forty years. These totalled 16,650 males and 14,150 females taken at all times of the year. The data were plotted by month and sex, the peaks in each length-frequency distribution being assigned ages beginning from zero for the first peak in November (the normal date of pup release) and the following five months. The second peak appearing in the November to

April period and the first peak for the remaining months were designated as being the modal length for a dogfish one year old, with each subsequent peak representing an additional year of age. The length estimate at each year of age was taken as the average of the peak-frequency lengths for the six months either side of November.

In the calculation of growth curves from both the X-ray spectrometry and length-frequency data, the total length at birth was taken as 26.2 cm (n = 46) for males and 25.4 cm (n = 37) for females. This starting point was based on length measurements of pups (with no yolk sac remnants) extracted from full term females in November, 1972. the normal month of parturition (Chapter 3).

Growth in captivity:

Dogfish reared in captivity were caught in bottom trawls or by longlining in the Strait of Georgia during 1972 to 1974. Efforts to maintain the adult and immature animals in captivity were unsuccessful. Though many pups (taken from females at full term) died soon after removal from the uterus, five survived for up to 1 1/2 years in 0.6 x 1.2 x 0.9 m deep indoor tanks in which mean salinity was roughly 30 ppt, mean temperature close to 10 C, and an artificial day length approximating that outdoors. Their lengths were recorded monthly.

Length-weight analysis:

To provide data for growth in weight, length-weight data were collected on 535 dogfish as soon after capture as possible. Dogfish were measured to the nearest cm total length and 10 gm total weight. Since mature females often aborted pups or eggs when caught, the weight of the remaining ovarian and uterine eggs, and pups was subtracted to yield a minimum body weight. As the weight of mature females also varied during the year due to pup and ovarian egg growth, maximum body weight data for specific lengths were calculated by adding the weight of a mean number of eggs and pups normally carried by full term females of that length (Ketchen 1975 and my unpublished data from a related study). The dogfish used, though predominantly larger animals, were from the entire size range of each sex.

RESULTS

In dogfish vertebrae, calcium and phosphorus were the only elements clearly separated by the X-ray spectrometric method (Fig.2-2). The changes in concentration of these elements across the vertebrae of an adult male dogfish are shown in Fig.2-3. At the ends of each scan the concentration of both elements was nearly undetectable as the electron beam struck the surrounding cartilage. To determine sample repeatability, the patterns of elemental composition within the vertebrae were ascertained twice, with the second scan lying roughly horizontally at right angles to the first. In each

Fig. 2-2: Typical data plot for a single 100-second analysis within the embedded area of a dogfish vertebra. P = phosphorus, Cl = chlorine, K = potassium, and Ca = calcium (Kα and Kβ are different X-ray emmission energies for the same element resulting from replacement of electrons dislodged by the microscope beam by ones from different orbitals).

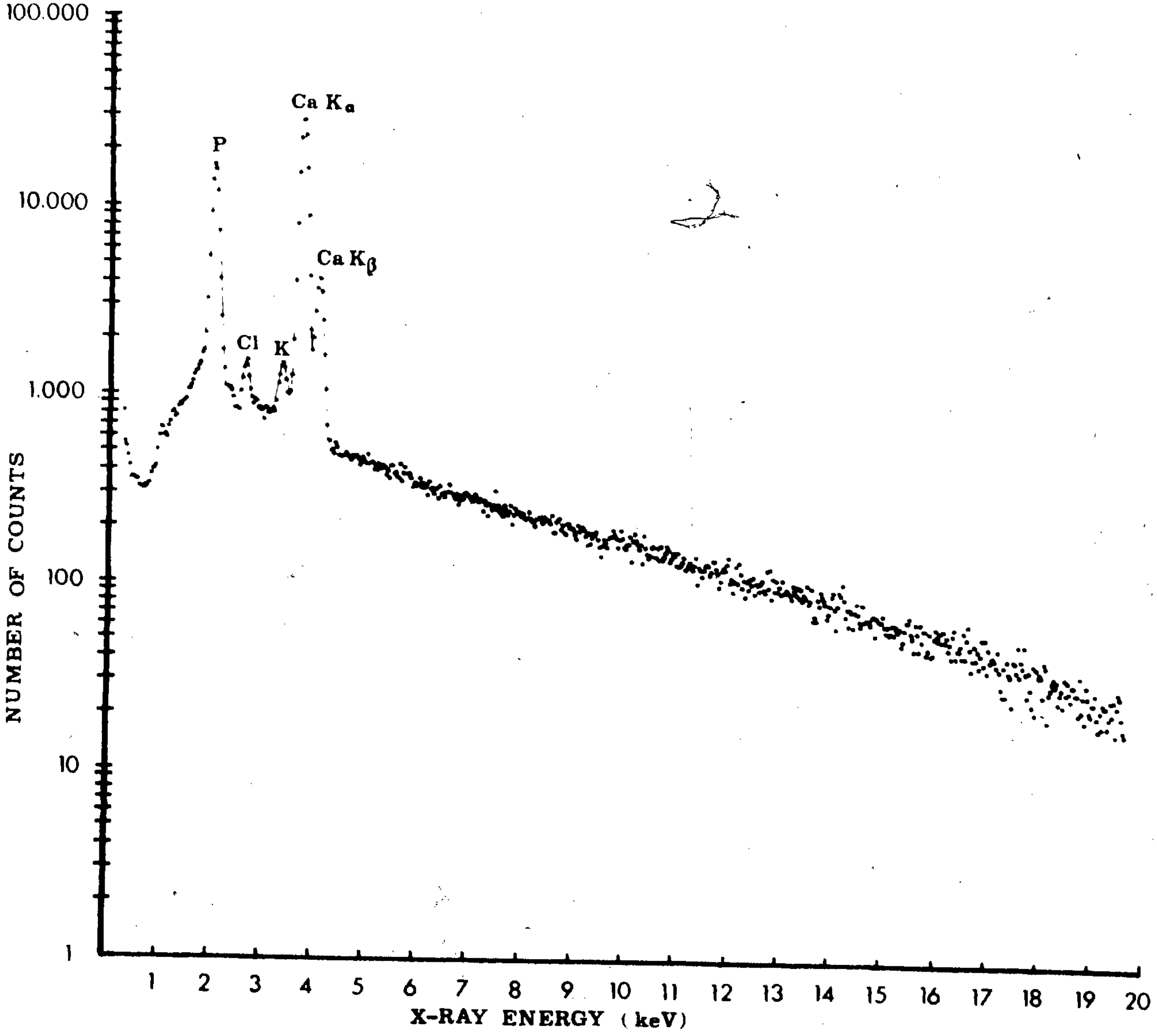
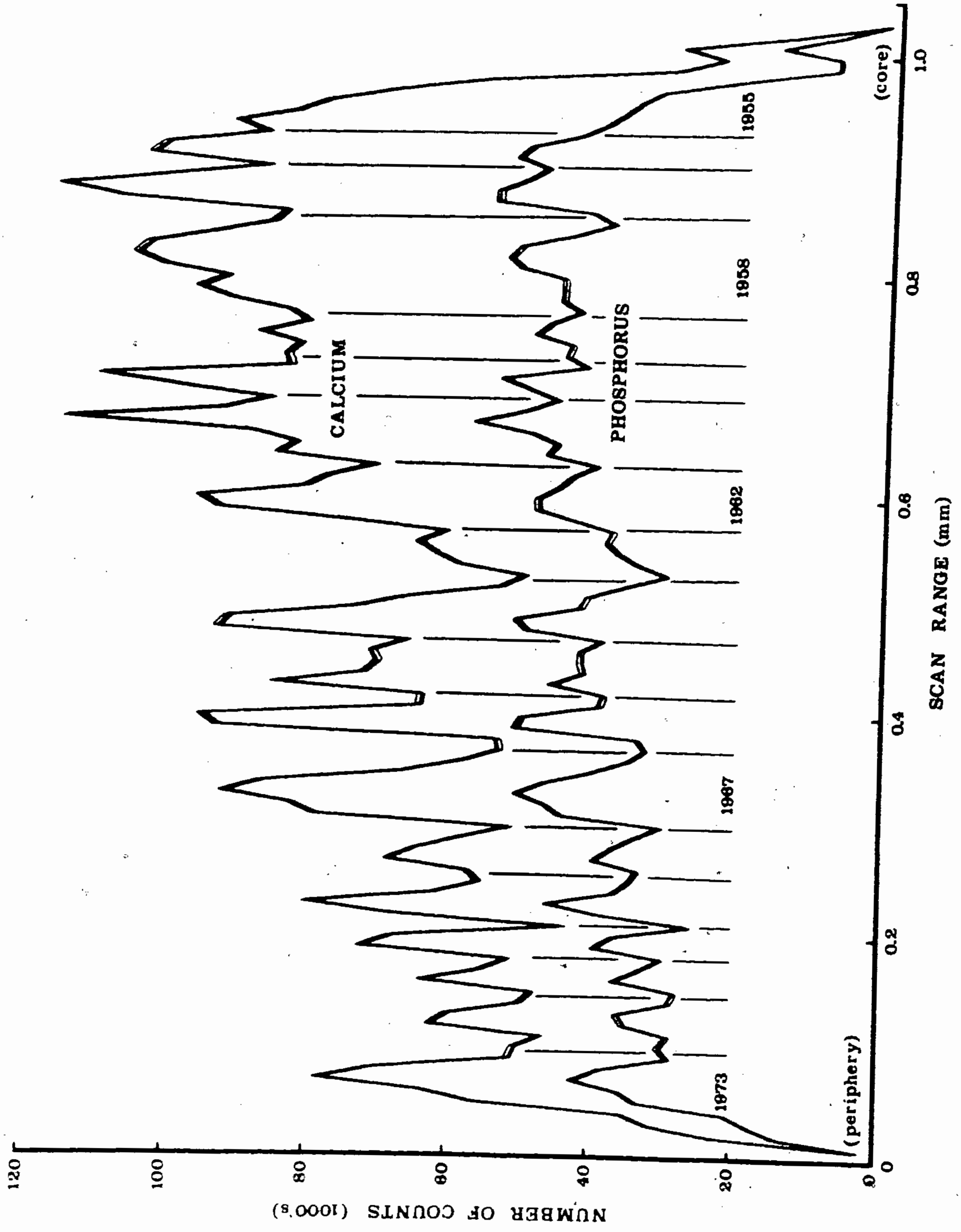

100.000
10.000
1.000
100
10
1
NUMBER OF COUNTS
P
Ca K_α
Ca K_β
Cl
K
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
X-RAY ENERGY (keV)

Fig. 2-3: Elemental count pattern for CaKα and P in the vertebra of an 83 cm Strait of Georgia male dogfish. Confidence limits of 95% as derived by text method exist about each curve, but are only evident on peaks and troughs. Dates are derived by equating the peripheral peak as the last complete year of growth, and working backward through subsequent peaks. Since the young are normally released in November, and this animal was caught in June, 1974, an age of 20.6 years is suggested.


CALCIUM
PHOSPHORUS
1973
1967
1962
1958
1955
(periphery)
(core)
NUMBER OF COUNTS (1000's)
0
20
40
60
80
100
120
SCAN RANGE (mm)
0
0.2
0.4
0.6
0.8
1.0

case the number of peaks determined were identical in any one vertebra.

Male and female age-length relationships derived from X-ray spectrometry age determination are shown in Fig. 2-4. Von Bertalanffy growth equations were fitted to these data and the age-length data derived from length-frequency analyses. The equations have the following form:

$$l_t = L_{max}[1-e^{-K(t-t_o)}]$$

where l_t = length at time t, L_{max} = theoretical mean maximum length, K = growth constant which indicates the rate at which length approaches L_{max}, and t_o = calculated time at which length equals zero. The values for these terms were computed by the iterative method of Allen (1966) and are presented in Table 2-1 in comparison to those obtained for other northeastern Pacific populations of dogfish. A comparison of growth rates determined from length-frequency data, reproductive data, and von Bertalanffy equations derived by X-ray spectrometry and other methods for specific size ranges, is shown in Table 2-2. Growth rates determined from reproductive data involved a comparison of mean lengths of females carrying a given number of large ovarian eggs in one year with mean lengths of those carrying the same number of first year embryos in the succeeding year.

Fig. 2-4: X-ray spectrometry age estimates for (A) male and (B) female dogfish in the Strait of Georgia. Von Bertalanffy growth curves are fitted to these data (2) and compared to curves derived from length-frequency data (1; this study) and spine circuli counts (3; Ketchen 1975).

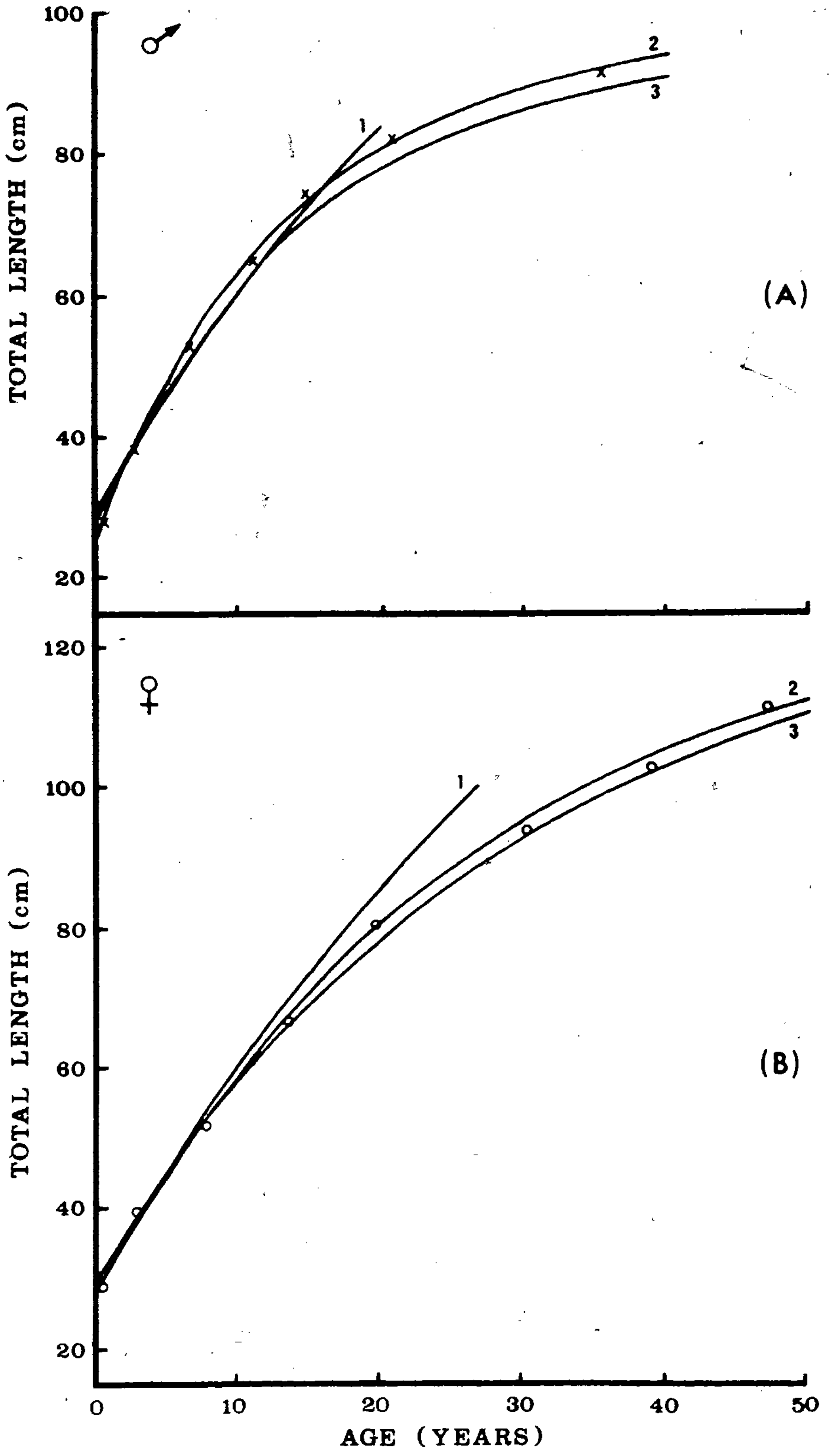

♂
(A)
1
2
3
100
80
60
40
20
TOTAL LENGTH (cm)
♀
(B)
1
2
3
120
100
80
60
40
20
TOTAL LENGTH (cm)
0
10
20
30
40
50
AGE (YEARS)

Table 2-1: Comparison of estimated von Bertalanffy growth equation terms based on various methods of age determination for spiny dogfish stocks in the northeastern Pacific.

Area/Source	Sex	K	L_{max}(cm)	t_o(yr)
Strait of Georgia:				
(a) X-ray spectrometry	M	0.072	98.4	-4.1
	F	0.037	128.0	-6.6
(b) Length-frequency[a]	M	0.027	163.0	-7.1
	F	0.018	215.9	-7.8
(c) Spine circuli	M	0.067	96.1	-5.0
(Ketchen 1975)	F	0.034	129.1	-7.3
Hecate Strait:				
Spine circuli	M	0.092	84.7	-3.7
(Ketchen 1975)	F	0.031	125.1	-10.6
British Columbia coast:				
Ketchen (1975)[b]	M	0.070	99.8	-4.7
	F	0.048	125.3	-4.9
Washington coast:				
Spine circuli	M	0.071	101.8	-5.2
Bonham et al.(1949)[c]	F	0.036	152.9	-6.7

[a] Roughly 25% of data included from southwest coast of Vancouver Island.

[b] The estimate for females is a composite derived from length-frequency and reproductive data of Ketchen (1975) for British Columbia waters, and length-frequency data of Bonham et al.(1949) for the Washington coast. For males, the estimate is an average derived from spine circuli data of Ketchen (1975) for the Strait of Georgia and Bonham et al.(1949).

[c] Equation terms provided in Ketchen (1975).

Table 2-2: Comparison of female spiny dogfish growth rates determined from length-frequency data, reproductive data, and von Bertalanffy equations derived from other methods of determining changes in length with increasing age.

Area/Source	Mean annual growth increment per length range (cm)			
	44-70	74-79	82-87	90-105
Strait of Georgia:				
(1) This study				
(a) length-frequency	2.7	2.5	2.4	2.2
(b) X-ray spectrometry	2.6	1.9	1.6	1.0
(2) Ketchen (1975)				
(a) length-frequency[a]	-	2.0	1.5	-
(b) spine circuli	2.4	1.8	1.5	1.0
(c) reproductive data[b]	-	-	-	1.0
Washington coast:				
Bonham et al.(1949)				
(a) length-frequency	3.3	-	-	-
(b) spine circuli	3.4	2.6	2.3	1.9

[a] Also had birth, first, and second year length-frequency modes indicating annual increments of 4.8 and 6.0 cm for the first and second years at large, respectively.

[b] Comparison of mean lengths of females carrying a given number of large ovarian eggs in one year with mean lengths of those carrying the same number of first-year embryos in the succeeding year.

Limited data from studies of growth in captivity in the first year of life for male and female pups are shown in Table 2-3 and compared to first year growth computed from the von Bertalanffy equations. The growth rate during the early years of dogfish life as derived from length-frequency data is found in Fig. 2-5.

The relationships of total length and body weight for male and female dogfish were derived by the allometric method of Pienaar and Thomson (1969) and are illustrated in Fig. 2-6. The lower curve (A) is for immature or barren females. The upper branch (B), for pregnant females, begins at 76 cm, the shortest length at which a mature female has been observed (Ketchen 1972). The difference between these two curves is the mean weight of eggs and pups carried by a full term female. The equations and other sampling data shown in Table 2-4 are compared with data from similar studies on both the east and west coasts of North America.

DISCUSSION

Elasmobranch age determination has been attempted in various ways. The only method available, other than tagging or length-frequency analysis, which are time consuming, expensive, or inaccurate techniques, has been visual examination of patterns of deposition in hard tissue. In elasmobranchs spines are uncommon, teeth are constantly renewed, scales are diminutive, and most of the

Table 2-3: Comparison of first year growth of spiny dogfish in captivity with those estimated from von Bertalanffy growth curves.

Area/Source	Males			Females		
	Length at birth(cm)^{a}	First year growth(cm)	Relative increase(%)	Length at birth(cm)^{a}	First year growth(cm)	Relative increase(%)
Strait of Georgia:						
(a) Growth in captivity	25.5	7.8^{b}	30.6	24.7	6.9^{c}	27.9
(b) X-ray spectrometry	25.2	5.0	19.8	27.7	3.7	13.4
(c) Length-frequency	28.4	3.6	12.7	28.3	3.3	11.7
(d) Ketchen (1975)	27.4	4.4	16.1	28.4	3.3	11.6
Hecate Strait:						
Ketchen (1975)	24.4	5.3	21.7	35.0	2.8	8.0
British Columbia coast:						
Ketchen (1975)	28.0	4.8	17.1	26.3	4.6	17.5
Washington coast:						
Bonham et al.(1949)	31.4	4.9	15.6	32.8	4.8	14.6

[a] Length at birth as determined for Strait of Georgia dogfish equals 26.2 cm for males and 25.4 cm for females.

[b] Based on 3 pups surviving an average of 11 months.

[c] Based on 2 pups surviving an average of 5 months.

Mean growth estimates from b and c are weighted by individual survival time.

Fig. 2-5: Early life growth rates of male and female dogfish from the Strait of Georgia as determined from length-frequency data. Curves are fitted by eye.

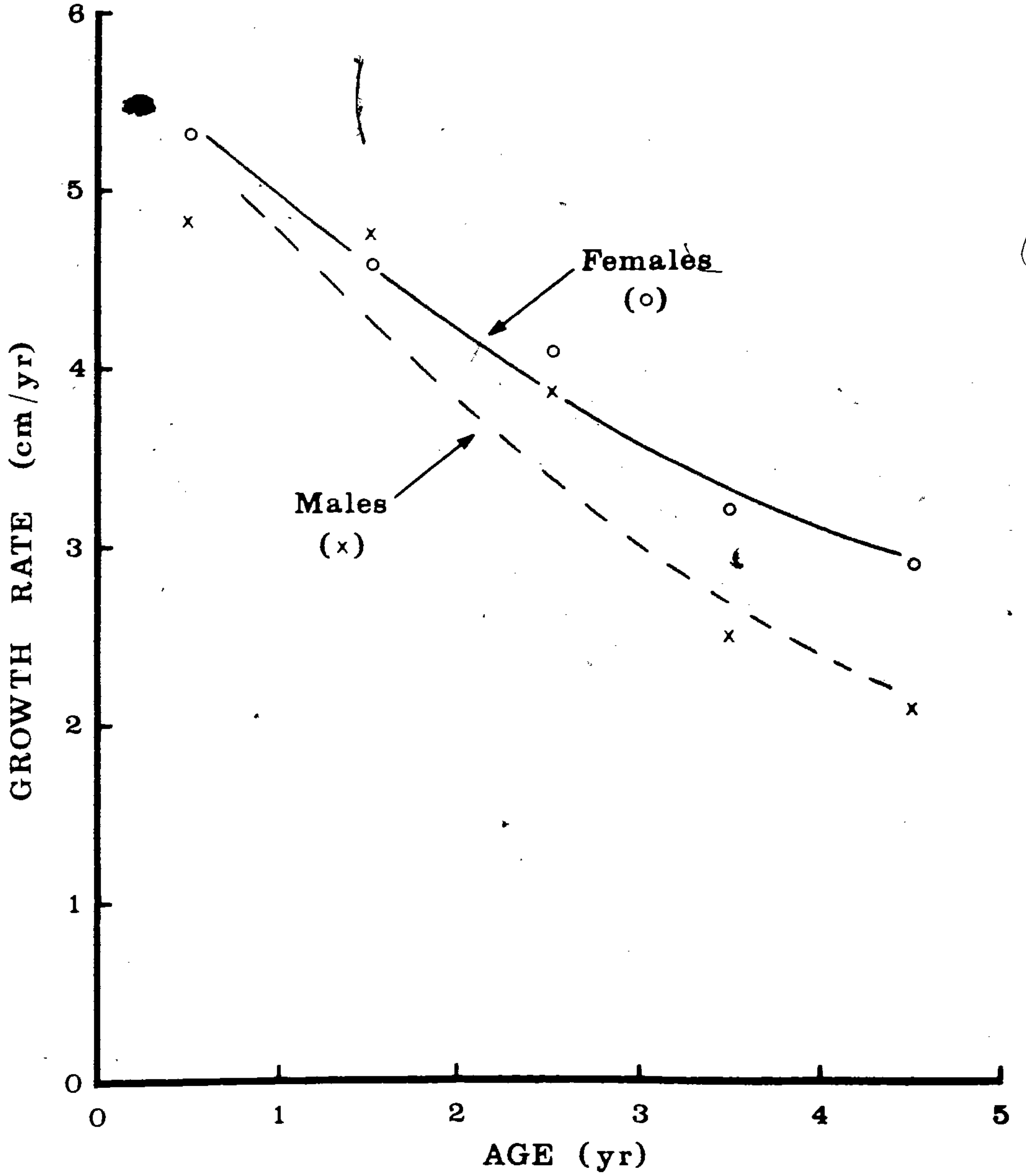

GROWTH RATE (cm/yr)
6
5
4
3
2
1
0
AGE (yr)
0
1
2
3
4
5
Females
(o)
Males
(x)

Fig. 2-6: Length-weight relationships for male and female dogfish from the Strait of Georgia. For females two curves are presented above the 50% sexual maturity length of 93.5 cm (Ketchen 1972). The lower one (A) representing animals with no eggs or pups, and the upper one (B) with full term pups and ripe eggs. At any one time the weight of a mature female should lie on or between these two curves. W = weight in grams, L = length in mm.

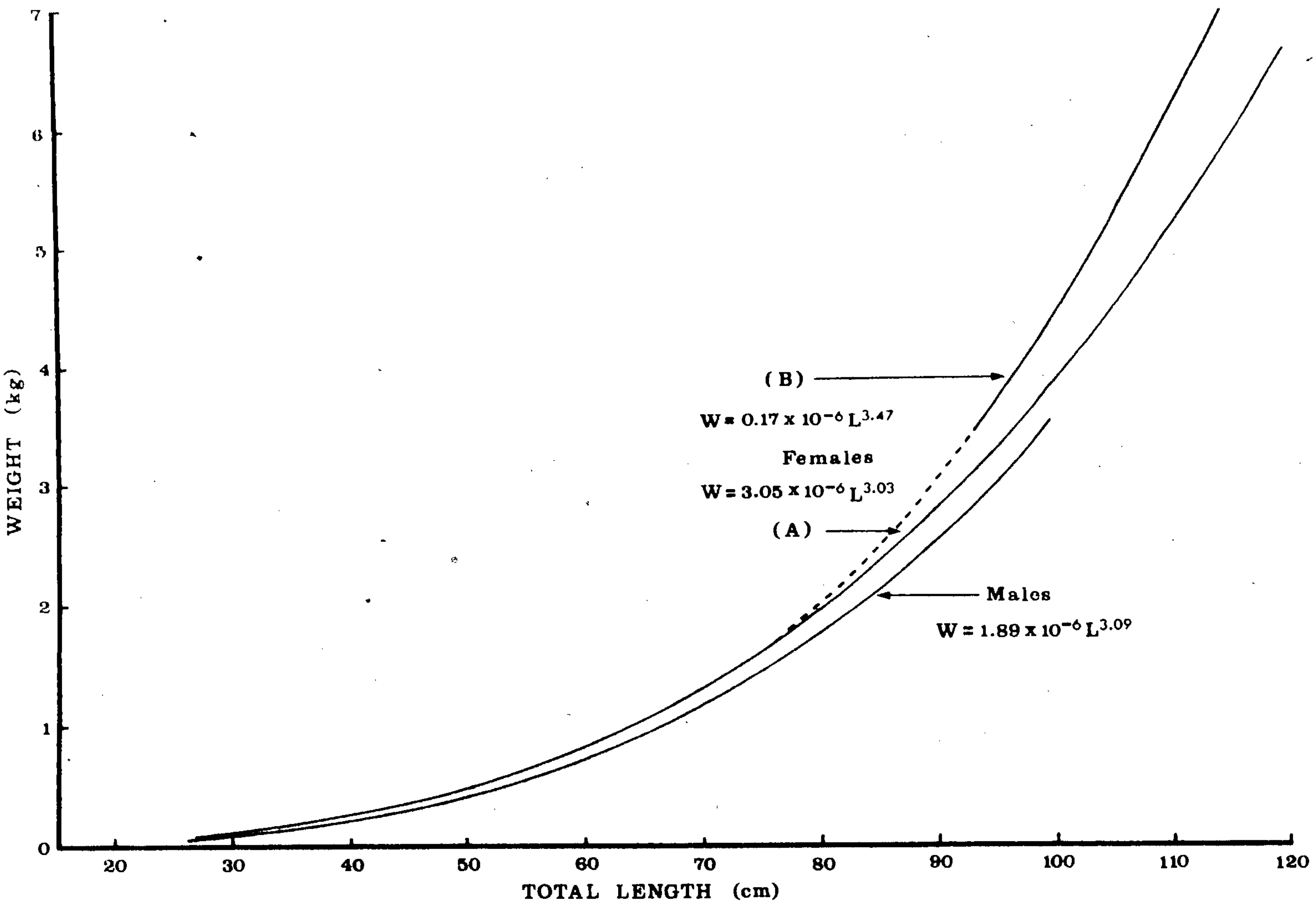

(B)
W = 0.17 x 10⁻⁶ L3.47
Females
W = 3.05 x 10⁻⁶ L3.03
(A)
Males
W = 1.89 x 10⁻⁶ L3.09
WEIGHT (kg)
0
1
2
3
4
5
6
7
TOTAL LENGTH (cm)
20
30
40
50
60
70
80
90
100
110
120

Table 2-4: Comparison of length-weight relationship data for spiny dogfish on the east and west coasts of North America.

Area/Source	Number sampled	Size range in sample(cm)	Equation (gm/mm)[a]
West coast:			
Strait of Georgia:			
(a) males	259	26-98	$W = 1.89x10^{-6}\ L^{3.09}$
(b) females(no pups or eggs)	276	27-120	$W = 3.05x10^{-6}\ L^{3.03}$
(c) females (full term)	10	93-120	$W = 0.17x10^{-6}\ L^{3.47}$
San Francisco Bay (Razum 1952)			
sexes combined	137	15-93	$W = 7.15 \times 10^{-6}\ L^{2.89}$
East coast:			
New Brunswick (Kohler et al.1969)[b]:			
(a) males	207	48-84	$W = 15.24x10^{-6}\ L^{2.78}$
(b) females	217	48-97	$W = 0.85x10^{-6}\ L^{3.23}$
(c) sexes combined	424	48-97	$W = 1.73x10^{-6}\ L^{3.12}$
Rhode Island (Jensen 1966):			
sexes combined	210	28-94	$W = 0.60x10^{-6}\ L^{3.27}$

[a] Calculated by method of Pienaar and Thomson (1969). Length-weight graphs but no data are found in Pugsley (1940) and Bonham et al.(1949) for the west coast, and Templeman (1944) for the east coast.

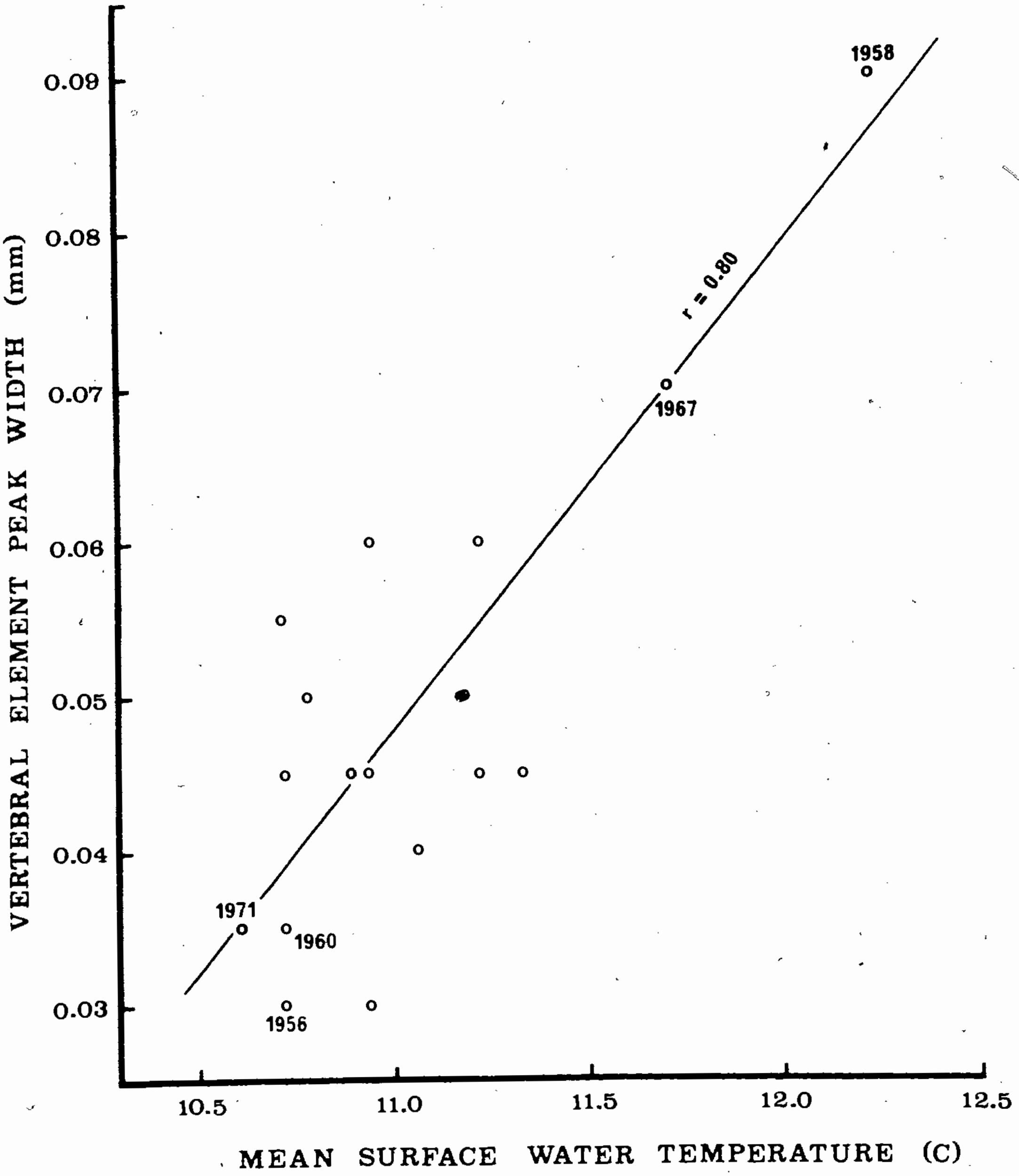
[b] Equations transformed from lbs. and cm.

skeleton is cartilage. Calcified vertebrae are the only hard tissue components consistently present. Ishiyama (1951), Diaber (1960) and Berry (1965) noted circuli in vertebral cross-sections of skates, as did Haskell (1949), Aasen (1963), and Stevens (1975) for several species of sharks. However, I did not observe vertebral circuli in spiny dogfish, which is consistent with the observation of Kaganovskaia (1933, 1937) for this particular species. Since growth of the elasmobranch skeleton is a one-way process of deposition (Simkiss 1974), and no internal remodelling or resorption of this store of minerals apparently occurs, any seasonal or annual variation in deposition might be detectable by X-ray spectrometry and provide a measure of age.

In this study, cyclic patterns of calcium and phosporus concentrations in vertebrae of Squalus acanthias were observed (Fig.2-3) which suggested seasonal changes in rates of deposition. Some confirmation of this postulate was obtained by comparison of ages of young dogfish estimated from X-ray spectrometry with those derived from length-frequency data. Individuals which length-frequency data indicated were one and three years old exhibited single and triple peaks of calcium and phosphorus in their vertebrae, thus indicating a yearly period in these changes. To further examine this observation, the temporal and spatial variation of the chosen elements in the environment, and the possible effect of climatic fluctuations on uptake were considered. In British Columbia coastal waters phosphorus concentrations characteristically exhibit winter maxima and summer minima, while calcium, which is relatively abundant, remains practically constant. Hence, phosphorus appears to have a yearly period. Since the X-ray spectrometric patterns of calcium and phosphorus (Fig.2-3) are similar, possibly because phosphorus may have some direct bearing on the uptake of calcium (Love 1970), the regular changes in calcium also appear to be annual, suggesting that age may be estimated by counting the peaks.

The widths of peaks (expressed as distance between adjacent minima) also varied. Since dogfish are poikilothermous these differences could reflect seasonal temperature changes during the main periods of growth. To examine this hypothesis, dates were assigned to each peak by equating the peripheral one as the last complete year of growth, and assigning years to each previous peak. Though the depths dogfish inhabit are poorly known, when peak widths are compared (Fig.2-7) with mean annual surface water temperature at Departure Bay, B.C., the area with records closest to that from which the dogfish were taken, a significant correlation was found ($r = 0.80$, $P < 0.001$, $N = 18$). In warm years such as 1958 and 1967 the peak widths were distinctly wider than in cooler years (1956, 1960, and 1971). However, the mean temperature difference among these years is less than 2 C. Since these differences are small, temperature may not be acting directly to affect elemental deposition, but via some indirect way.

Fig. 2-7: Relationship between vertebral element peak width (distance between adjacent minima) as determined by X-ray spectrometry for the dogfish noted in Fig. 2-3 and mean annual surface water temperature at Departure Bay, B.C.


VERTEBRAL ELEMENT PEAK WIDTH (mm)
0.09
0.08
0.07
0.06
0.05
0.04
0.03
MEAN SURFACE WATER TEMPERATURE (C)
10.5
11.0
11.5
12.0
12.5
r = 0.80
1958
1967
1971
1960
1956

Since the spiny dogfish also has circuli on its dorsal spines, various studies have used these as measures of age (Kaganovskaja 1933, 1937; Bonham et al.1949; Holden and Meadows 1962; Ketchen 1975). The limitations of spine readings and the tentative nature of conclusions drawn from them have been reviewed by Ketchen (1975). The relationship of length to estimated age as deduced from X-ray spectrometry (Fig. 2-4), though based on relatively few samples, is similar to that of Ketchen (1975) derived from second dorsal fin spine circuli counts from Strait of Georgia dogfish. Values for the terms in the von Bertalanffy equations calculated from spine data (Table 2-1) are sufficiently close to be within the limits of error for the X-ray spectrometry method.

The curves describing the age-length relationship as determined from length-frequency data (Fig.2-4) correspond with the X-ray spectrometry curves for only the first 18 and 11 years for males and females respectively. These differences may result from the difficulty of distinguishing frequency peaks in larger fish, thus leading to an underestimate of age and consequently a higher estimate of growth rate. In addition, roughly 25% of my length-frequency data came from the southwest coast of Vancouver Island, which could have resulted in incorporation of data from dogfish with different growth rates. In Table 2-2 growth rates for female dogfish derived from length-frequency analyses and reproductive data are compared with rates calculated from von Bertalanffy equations derived from data based on other ageing methods. Though the rates derived from length-frequency data in this study were higher than those of X-ray spectrometry, they were similar to those of Bonham et al.(1949). However, their spine circuli count method may also have produced an underestimate of age and a resultant overestimate of growth rate since they did not compensate for possible missing circuli from worn spine tips (as was done in Ketchen 1975), and had fewer data from larger animals as spines which were difficult to read were rejected. Growth rates derived from von Bertalanffy equations for the X-ray spectrometry data and the spine data of Ketchen (1975) differ most significantly at smaller sizes, and can be accounted for by the greater departure of Ketchen's calculated length at birth (Table 2-3) from the observed mean size. His length-frequency data and reproductive data growth rates compare favourably with those derived from X-ray spectrometry.

The values for von Bertalanffy equation terms for the curves presented in Fig.2-4 re-emphasize the differences among the various age determination methods. These results from the Strait of Georgia are compared (Table 2-1) with results from Hecate strait, all British Columbia waters (Ketchen 1975), and the Washington coast (Bonham et al.1949). With the exception of values from length-frequency data, the values for most areas are similar. The extreme values for males are L_{max} and K for Hecate Strait. However, as Ketchen (1975) points out, the largest male in his sample was 89 cm, although I have recorded Hecate Strait males up to 98 cm. If L_{max} was increased accordingly a corresponding decrease in K would result, placing it close to values for other areas. For females the most aberrant data are the Hecate Strait estimate for t_0 , the British Columbia estimate for K, and the estimate of L_{max} for the Washington coast. Ideally, the term t_0 should reflect the period of gestation, which in the case of dogfish is 1.9 yr (Chapter 3). However. all t_0 terms in Table 2-1 have negative values which are longer than the gestation period. The von Bertalanffy equation assumes that growth follows a uniform pattern from conception to death, an unlikely situation. A large negative value for t_0, such as found for Hecate Strait females, thus indicates a poorer fit of the von Bertalanffy curve during the early part of life. In the British Columbia composite data, K is nearly one-third larger than that of the other curves. This term is derived from Ketchen's (1975) length-frequency and reproductive data (Table 2-2), and the length-frequency data of Bonham et al.(1949), a total of only six points. Considering the probable over-estimation of growth rate from length-frequency data, such a higher K value would be expected. Similarly, L_{max} for females on the Washington coast is considerably larger than the other estimates, closely approximating the 160 cm length indicated for the largest female caught in adjacent British Columbia waters (Clemens and Wilby 1961). However, my data and those from the Pacific Biological Station for British Columbia waters indicate maximum lengths of 130 cm and 103 cm for females and males respectively. These figures are more in keeping with values predicted from the von Bertalanffy equations.

Holden (1973) noted a fairly constant relationship of length at 50% sexual maturity (l_m) to maximum length (L_{max}) both within a species and in elasmobranchs generally. For S. acanthias females from the northeastern Atlantic this ratio was 0.76, meaning that the average female matured at 76% of her ultimate maximum length. For Strait of Georgia females, using 93.5 cm (Ketchen 1972) for l_m and 128.1 cm for L_{max} as calculated from X-ray spectrometry data, the ratio is 0.73. On the other hand, the ratio for the Washington coast females is 0.61, which exceeds the 95% confidence limits (0.64-0.90) for all 20 elasmobranch species listed (Holden 1973), further suggesting that the Washington L_{max} is too high. Considering that all Ketchen's (1975) analyses of female growth support his Strait of Georgia data over that of Bonham et al.(1949), it appears questionable that the Washington data should be included in his composite equations for British Columbia waters. The validity of the British Columbia composite equations therefore seem doubtful since the data of Bonham et al.(1949) are included. I suggest that von Bertalanffy equations calculated from age-length data determined by X-ray spectrometry and Ketchen's (1975) spine data, which have values of $K = 0.070$, $L_{max} = 97.3$ cm, and $t_0 = -4.5$ yr for males, and $K = 0.036$, $L_{max} = 125.5$ cm, and $t_0 = -6.9$ yr for females, better describe dogfish growth in the Strait of Georgia.

The dogfish growth data derived from von Bertalanffy equations permits a comparison of the estimated length at birth and the rate of growth during the first year (Table 2-3). In general, predicted length at birth was higher than the 26.2 cm for males and 25.4 observed for females, indicating a poorer fit of the von Bertalanffy equations in this size range. The X-ray spectrometry data for males indicated 5 cm growth during the first year, a relative increase in length of 20%. Length-frequency data (Fig.2-5) also indicated a 5 cm growth during the first year for both sexes and a decrease to 2-3 cm/yr by the fifth year of life. Young dogfish kept in captivity grew nearly 7.5 cm in their first year (a relative increase of 30%), thus indicating a capability for growth not expressed in nature.

Since change in length of any one dogfish is usually less variable than weight as a measure of growth in relation to age, it has been used in this and other studies. However, as most other studies were restricted in the size ranges sampled, my work was designed to provide more accurate data on growth in weight as a function of length. For this purpose, length-weight curves have been derived (Fig. 2-6). Dogfish females not only grew longer and heavier than males, but also were heavier per unit length, an observation previously reported by Pugsley (1940) and Bonham et al.(1949) for dogfish from the west coast of North America, and Templeman (1944) and Kohler et al. (1969) for east coast dogfish. In general, there is little difference between the length-weight relationships derived for the Strait of Georgia dogfish (Table 2-4), and those for other regions (above plus Razum 1952 and Jensen 1966) except for Pugsley (1940) whose limited numbers and restricted size range have biased his analysis. Although north Atlantic dogfish grow more rapidly (Holden and Meadows 1962), their length-weight relationships are similar to those of dogfish in the northeastern Pacific.

This study indicates that the X-ray spectrometry technique may provide a measure of age which can be used to estimate growth rates. However, the extent of its use obviously relates to the time and money available, since it is a time consuming procedure. For example, at the 100-second analysis rate it takes approximately one hour to scan the vertebra of a one-year old animal, and six hours for a 30-year old. However, it is possible that the analysis rate could be improved by using a continuous sample-stage movement in conjunction with an automatic analyser relay to a computer-plotter. This would reduce the time required and minimize human error. A system possibly adaptable to this use has been outlined by Dao (1974). Though age determination by X-ray spectrometry has been applied to spiny dogfish in this study, it might be applicable to other fish species where no alternative is more suitable. Theoretically, it might be used for determining the age of any organism possessing a hard tissue which has been subjected to environmental changes during its growth, provided the periodicity is known.

Chapter 3

REPRODUCTION AND EMBRYONIC DEVELOPMENT

INTRODUCTION

The dogfish shark is an ovoviviparous fish having a gestation period of almost two years and producing only half a dozen progeny per pregnancy. These reproductive characteristics make it particularly vulnerable to an intensive fishery such as occurred in British Columbia waters during World War II. In this case a dramatic stock reduction ensued (Barraclough 1948), illustrating the need for suitable reproductive data on which to base management decisions should a significant fishery for this species be re-established. Subsequent studies clarified many features of reproduction (Bonham et al. 1949, Ketchen 1972), but data on size distribution at maturity, timing of mating and breeding, and embryonic development were still meagre. This study was directed to filling these voids for Strait of Georgia dogfish.

MATERIALS AND METHODS

From August, 1973 to June, 1974, approximately 50 male and 50 female dogfish per month of length 65 to 123 cm were sampled from commercial troll catches from the Gulf Islands area of the Strait of Georgia, B.C., for reproductive analyses. This area is well known for its abundance of large dogfish which are here assumed to be representative of the size range of matures in the Strait.

To determine state of maturity and gametogenic timing for males, testes were initially preserved in 10% formalin and transferred to Bouin's solution prior to sectioning and staining with hematoxylin and eosin. For each month the mean proportions of ampullae containing each spermatogenic stage, as defined and illustrated for northeastern Atlantic dogfish by Simpson and Wardle (1967), were determined. These stages are:

(A) Spermatocytes

(B) Spermatids

(C) Spermatid metamorphosis

(D) Sperm in parallel bundles; no Sertoli bodies

(E) Ripe sperm in conical bundles; Sertoli bodies present

(F) Evacuated ampullae.

The counts involved determining the number of ampullae containing each stage on a straight line bisecting the testes joining the germ ridge and the region of efferent ductules. Mature males were defined as those possessing any number of evacuated ampullae.

Mature females were categorized in three pregnancy stages as having either: (a) Large ovarian eggs and flaccid uteri (between pregnancies), (b) "Candles" (gelatinous uterine capsules) containing embryos in early stages of development, or (c) Embryos free in uteri at later stages of development.

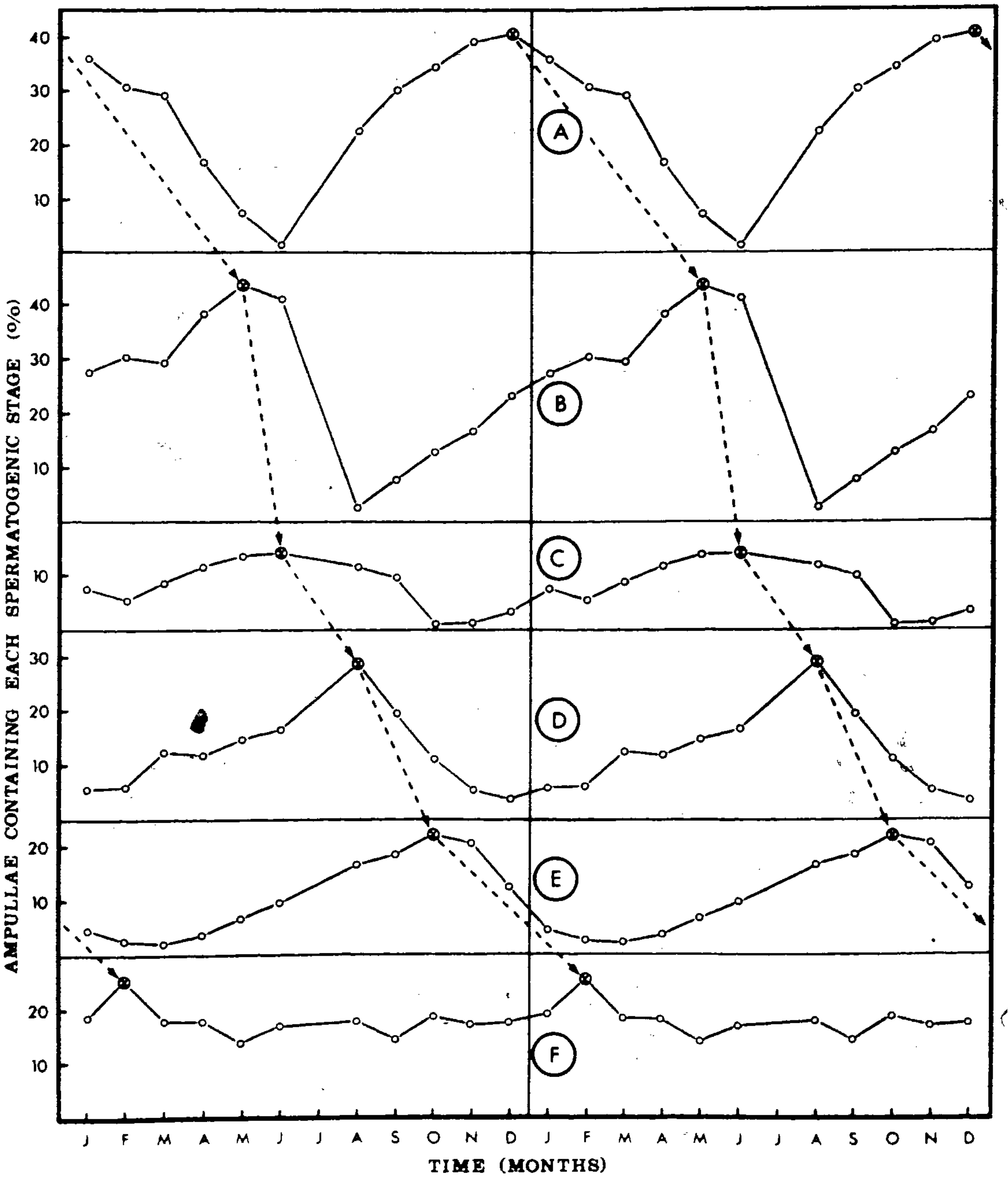
Length-frequency data necessary for determining modal length of mature dogfish were obtained from 8900 males and 6200 females whose lengths were at or greater than the mode among all samples of each sex. The modes, 84 cm for males and 94 to 96 cm for females, result from availability of fish to gear and gear selectivity when fishing for mature sizes. Though these data were collected with all types of gear, modal lengths for each type of gear fell within 83 to 84 cm and the distribution of lengths greater than the modes were similar, thus combination of data is not comsidered to bias the results. These data consisted of my plus those collected by staff of the Pacific Biological Station, Nanaimo, B.C., from the Strait of Georgia over the past forty years, although primarily (>80%) within the period 1969-1974.

Ovaries and embryos were preserved in 10% formalin. Mean diameters of developing eggs in the ovaries were determined by volumetric conversion. Mean length of embryos and volume of their external and internal yolk sacs were determined monthly.

RESULTS

The monthly variation in proportions of ampullae containing each spermatogenic stage for dogfish in the Strait of Georgia is shown in Fig.3-1 (n = 272). Here and after, data are plotted mid-monthly. The range of maturation sizes, determined from histological examination of testis development, indicated the shortest mature at 72 cm and the

Fig. 3-1: Seasonal variation in proportions of ampullae containing each spermatogenic stage in the testes of spiny dogfish in the Strait of Georgia over a 2 yr period. A = spermatocytes, B = spermatids, C = spermatid metamorphosis, D = sperm in parallel bundles with no Sertoli bodies, E = ripe sperm in conical bundles with Sertoli bodies present, and F = evaculated ampullae. Dashed lines join peak frequencies.


A
B
C
D
E
F
40
30
20
10
AMPULLAE CONTAINING EACH SPERMATOGENIC STAGE (%)
J F M A M J J A S O N D J F M A M J J A S O N D
TIME (MONTHS)

longest immature at 93 cm. The cummulative proportions mature as a function of length were plotted to derive the length at which 50% of male dogfish reach maturity and shown in Fig.3-2 in comparison to the relation between length and percentage maturity of females in British Columbia waters (Ketchen 1972).

To estimate modal lengths of mature dogfish, it is necessary to derive a female survivorship curve. The origin for this curve must be calculated from the number of embryos produced by the female breeding stock. Thus, the survivorship curve (Fig.3-3) must be constructed to determine the number of female embryos required to produce one breeding female at the modal length of mature females. Curve A is first fitted by eye to length-frequency data for lengths at or greater than the frequency mode resulting from availability to gear and gear selection, as these data are assumed to reflect the effects of natural mortality on numbers of dogfish with increasing age. This curve is extended linearly (dashed line) from the frequency mode to an arbitrary number of progeny at the length at birth. The relative numbers at birth (l_o) are then determined by an iterative method of balancing numbers of embryos produced by a breeding stock ($\Sigma l_x m_x$) and the number of breeding females (Σk_x) using the formula:

$$\frac{\Sigma l_x \; m_x}{[l_o] \quad \Sigma k_x} = 1$$

Fig. 3-2: Cummulative percentage of mature male dogfish in the Strait of Georgia as a function of length in comparison to the relation between length and percentage maturity of female dogfish in British Columbia waters (Ketchen 1972). The sizes at which 50% are mature, as indicated by presence of evacuated ampullae and embryos or mature ova, are shown.

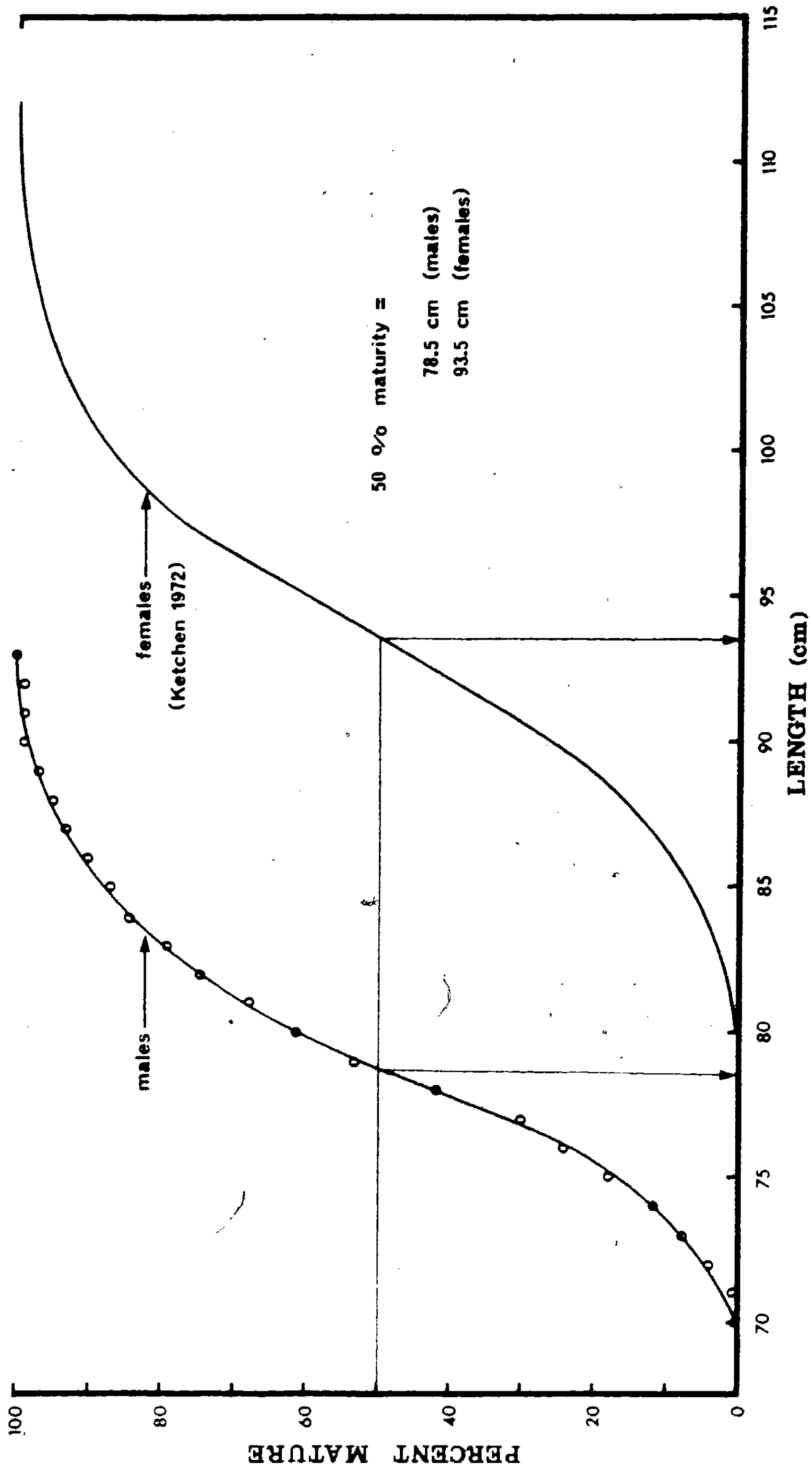
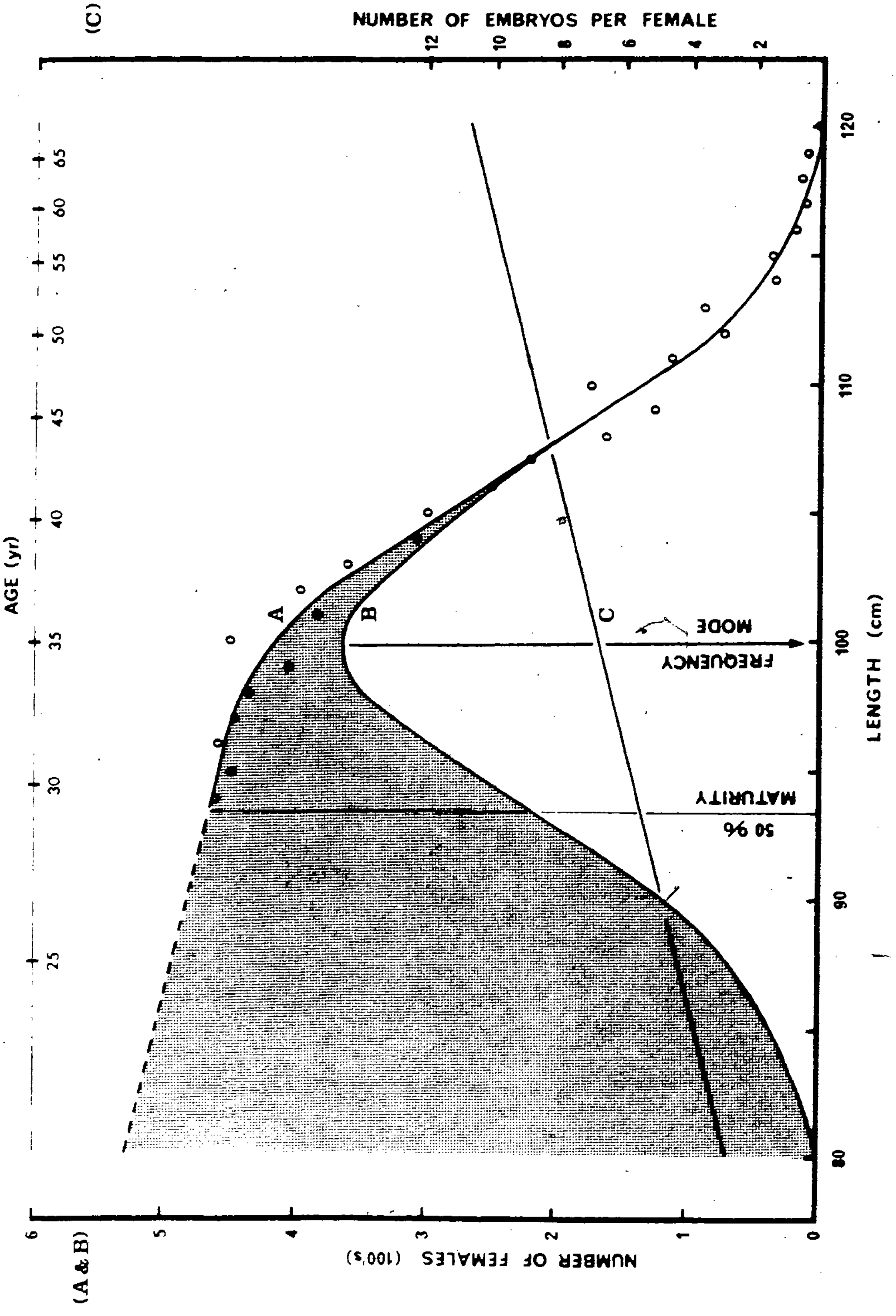

males
females (Ketchen 1972)
50 % maturity =
78.5 cm (males)
93.5 cm (females)
PERCENT MATURE
0
20
40
60
80
100
LENGTH (cm)
70
75
80
85
90
95
100
105
110
115

Fig. 3-3: Calculated length-frequency distribution of mature female dogfish in British Columbia waters to indicate modal length. Curve A is fitted by eye to length-frequency data (o); the dashed portion is part of an assumed survivorship curve. Curve B is derived from the application of Ketchen's (1972) data on maturity as a function of length (Fig.3-2) to curve A. Curve C, the number of embryos per female as a function of length (Ketchen 1972), is used to calculate the origin of the survivorship curve. Age axis at top of figure is calculated from von Bertalanffy growth equations in chapter 2. The shaded area represents presumed immature dogfish numbers.


(C)
NUMBER OF EMBRYOS PER FEMALE
12
10
8
6
4
2
AGE (yr)
25
30
35
40
45
50
55
60
65
A
B
C
FREQUENCY MODE
50 % MATURITY
LENGTH (cm)
80
90
100
110
120
NUMBER OF FEMALES (100's)
0
1
2
3
4
5
6
(A & B)

for the appropriate value of l_0 such that k (at modal length of mature females) = 1.00 (Table 3-1). In this equation, the terms are derived as a function of length and defined as follows:

(1) x - age class [as determined from von Bertalanffy growth equations in chapter 2].

(2) l_x - number of females surviving to beginning of age class [Curve A in Fig.3-3; l_0 = number at birth].

(3) m_x - number of female embryos per female per year [0.5(50:50 sex ratio) 0.5(2 yr gestation) j_x f_x].

(4) k_x number of females breeding per year [Curve B in Fig.3-3 = $2k_x$; 0.5(2 yr gestation) j_x l_x].

and in these,

(5) j_x - percentage distribution of mature females [Fig.3-2 (Ketchen 1972)].

(6) f_x - number of embryos per breeding female [Curve C in Fig.3-3 (Ketchen 1972)].

From term 4, $l_x = 2k_x/j_x$. Therefore, at k(mode) = 1.00, j(mode) = 0.88, and l(mode) = 2.27. By iteration the appropriate l_0 = 3.57 embryos as indicated in Table 3-1, a life table for female dogfish in British Columbia waters. The modal length for mature females can be observed at 100 cm in Fig.3-3. With a 50:50 sex ratio

Table 3-1: **Assumed life table for mature female dogfish in British Columbia waters. Values derived through age-length function of Chapter 2. Terms defined in text. ■ = mode.**

Age class x(yr)	**Total length** (cm)	**Number breeding** k_x	**Number surviving** l_x	**♀ embryos per ♀** m_x	**Total ♀ embryos** $l_x m_x$
0	25.4	0	3.57	0	0
20	79.6	0	2.88	0	0
21	81.4	0.03	2.84	0.02	0.06
22	83.1	0.05	2.81	0.04	0.11
23	84.7	0.09	2.77	0.06	0.17
24	86.2	0.13	2.74	0.10	0.27
25	87.7	0.21	2.70	0.16	0.43
26	89.2	0.27	2.67	0.23	0.61
27	90.6	0.35	2.63	0.33	0.87
28	91.9	0.48	2.60	0.47	1.22
29	93.2	0.62	2.56	0.66	1.69
30	94.5	0.69	2.53	0.77	1.95
31	95.7	0.77	2.49	0.91	2.27
32	96.8	0.86	2.46	1.06	2.61
33	97.9	0.97	2.41	1.27	3.06
34	99.0	0.99	2.35	1.37	3.22
35	100.1	■ 1.00	2.27	1.49	■ 3.38
36	101.1	0.98	2.17	1.56	■ 3.39
37	102.0	0.95	2.06	1.65	■ 3.40
38	103.0	0.88	1.90	1.71	3.25
39	103.9	0.82	1.73	1.79	3.10
40	104.8	0.76	1.60	1.85	2.96
41	105.6	0.71	1.46	1.93	2.82
42	106.4	0.64	1.32	1.97	2.60
43	107.2	0.59	1.18	2.03	2.40
44	108.0	0.53	1.07	2.06	2.20
45	108.7	0.47	0.96	2.10	2.02
46	109.4	0.42	0.85	2.14	1.82
47	110.0	0.37	0.74	2.17	1.61
48	110.6	0.31	0.63	2.22	1.40
49	111.3	0.26	0.52	2.26	1.18
50	111.9	0.23	0.45	2.29	1.03
51	112.5	0.19	0.38	2.32	0.88
52	113.1	0.17	0.34	2.35	0.80
53	113.6	0.15	0.30	2.37	0.71
54	114.2	0.12	0.25	2.40	0.60
55	114.7	0.10	0.19	2.43	0.46
56	115.1	0.08	0.17	2.45	0.42
57	115.6	0.07	0.14	2.47	0.35
58	116.0	0.06	0.12	2.50	0.30
59	116.5	0.05	0.10	2.52	0.25
60	116.9	0.05	0.09	2.54	0.23
61	117.3	0.04	0.07	2.56	0.18
62	117.7	0.03	0.06	2.58	0.15
63	118.1	0.03	0.05	2.60	0.13
64	118.5	0.02	0.04	2.62	0.10
65	118.8	0.02	0.04	2.63	0.11
66	119.1	0.02	0.03	2.65	0.08
67	119.5	0.01	0.03	2.67	0.08
68	119.8	0.01	0.02	2.69	0.05
69	120.1	0.01	0.02	2.70	0.05
70	120.4	0	0	2.71	0

$\Sigma k_x = 17.66$ $\Sigma l_x m_x = 63.03$

at birth, a similar survivorship curve for males would also begin at 3.57 embryos. Assuming that modal numbers of mature dogfish are similar for both sexes, then modal length of mature males (85 cm) can be determined by application of data on the distribution of maturity as a function of length (Fig.3-2) to the assumed survivorship curve (Fig.3-4).

The seasonal distribution of pregnancy stages for mature females is shown in Fig.3-5. Approximately half of the mature females would be 12 months out of phase with this distribution since they have a 2 yr gestation period.

The development of ovarian eggs to the time of ovulation is shown in Fig.3-6A. In Fig.3-6B the growth of the embryo to parturition is indicated, and the change in volume of the external and internal yolk sacs are presented in Fig.3-6C.

DISCUSSION

Certain features of the size distribution of mature dogfish in the Strait of Georgia were in doubt at the initiation of this study. Histological examination of testes indicated 50% of males to reach maturity at 78.5 cm body length (Fig.3-2). I did not determine the length when 50% of females reach maturity as Ketchen (1972) recently reported this to be 93.5 cm for females taken primarily from the

Fig. 3-4: Calculated length-frequency distribution of mature male dogfish in British Columbia waters to indicate modal length. Curve A is fitted by eye to length-frequency data (o); the dashed portion is part of an assumed survivorship curve. Curve B is derived from the application of Fig.3-2 data on maturity as a function of length to curve A. Age axis at top of figure is calculated from von Bertalanffy growth equations in chapter 2. The shaded area represents presumed immature dogfish numbers.

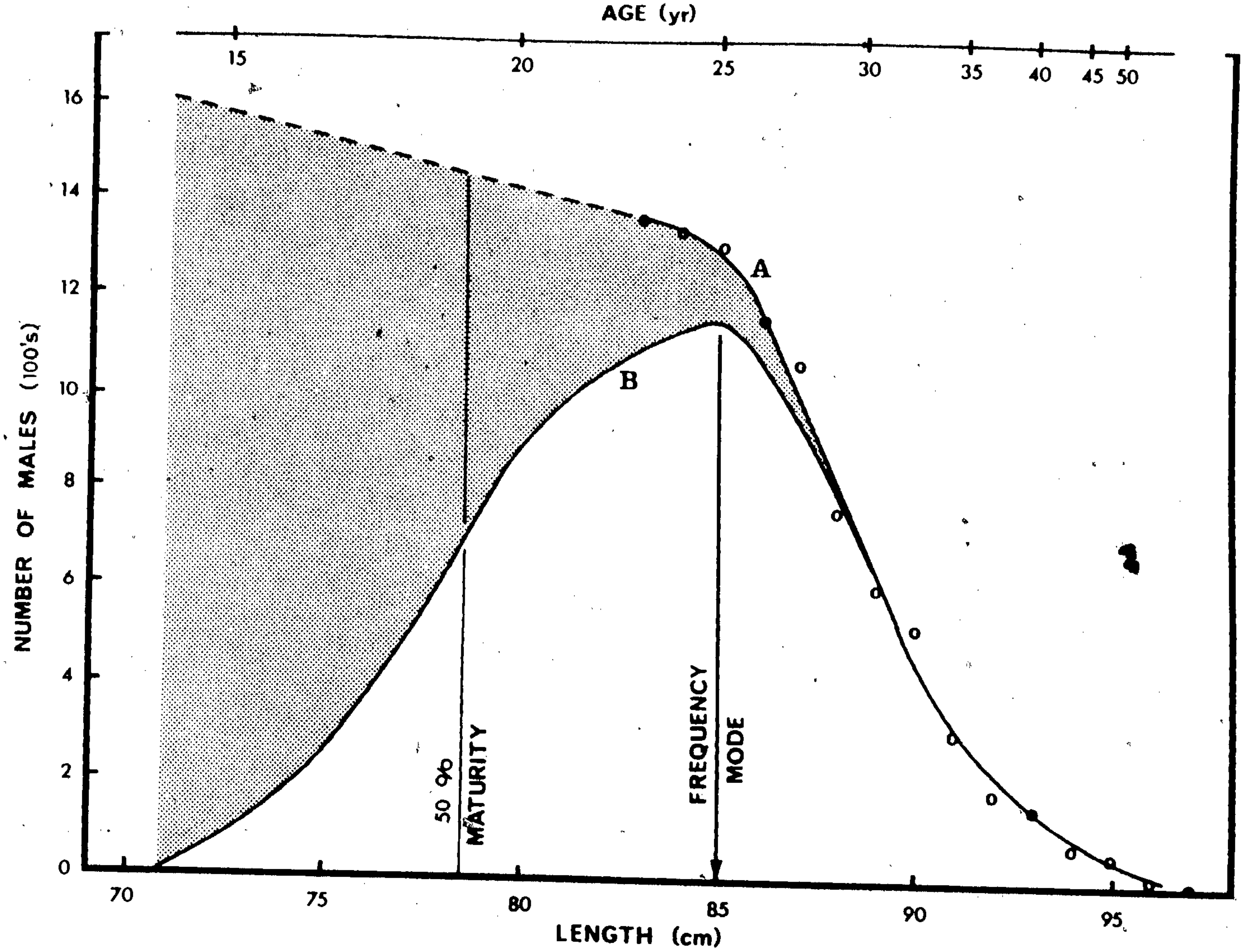

AGE (yr)
15
20
25
30
35
40
45
50
NUMBER OF MALES (100's)
0
2
4
6
8
10
12
14
16
A
B
50 %
MATURITY
FREQUENCY
MODE
70
75
80
85
90
95
LENGTH (cm)

Fig. 3-5: Distribution of pregnancy stages in Strait of Georgia mature female dogfish over the 2 yr gestation period. Candles are encapsulated uterine eggs in the early stages of embryological development. Females between pregnancies have released progeny but not yet ovulated.

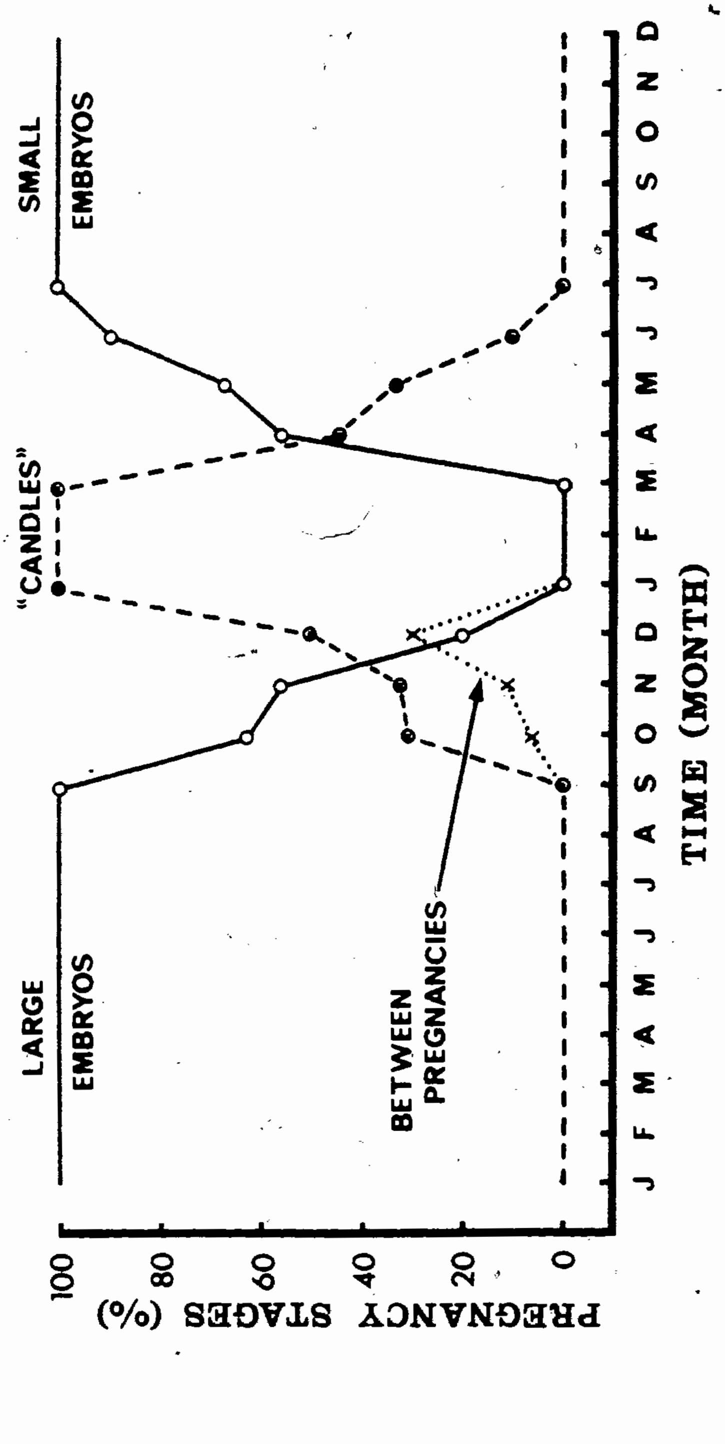
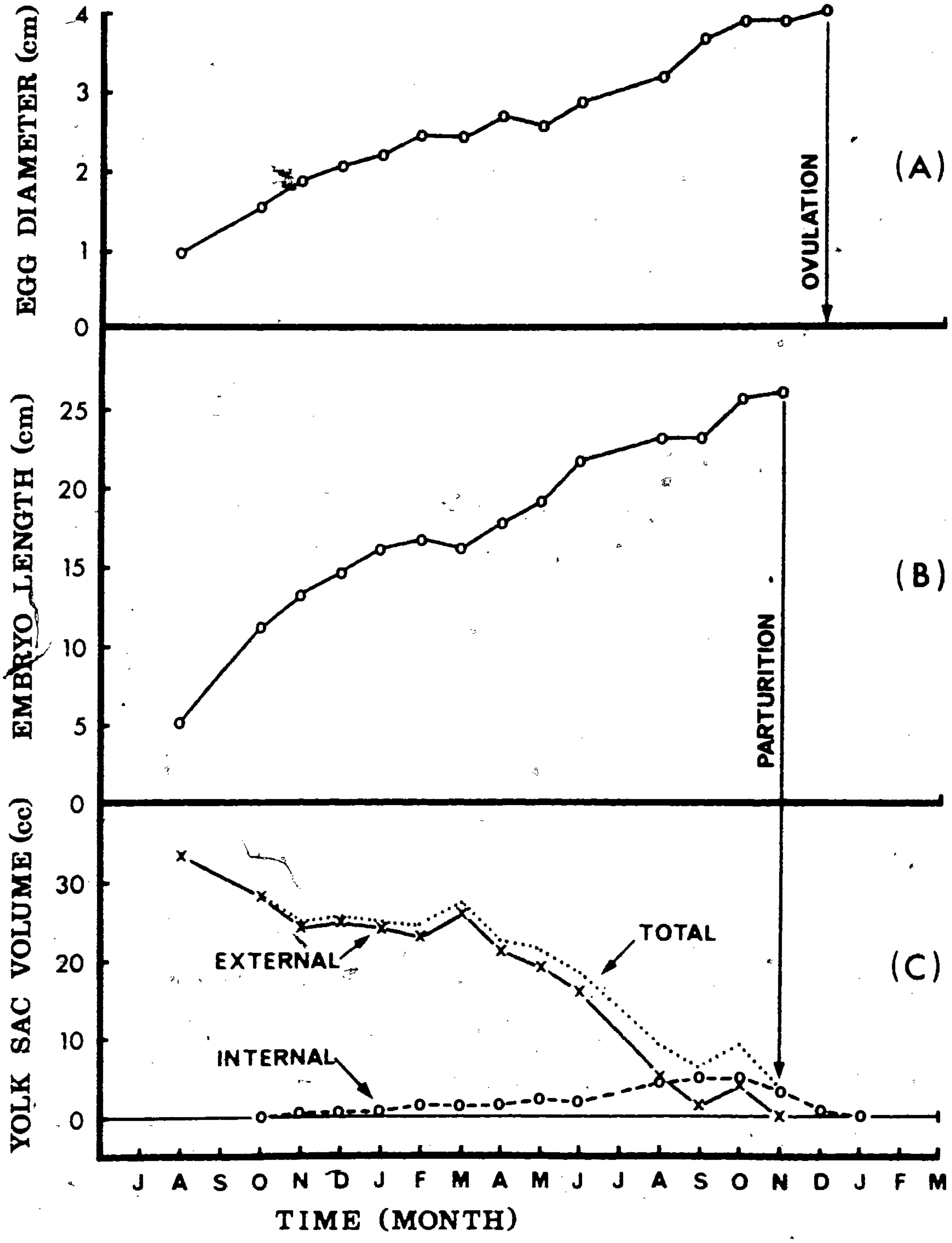

PREGNANCY STAGES (%)
100
80
60
40
20
0
J F M A M J J A S O N D J F M A M J J A S O N D
TIME (MONTH)
LARGE EMBRYOS
"CANDLES"
SMALL EMBRYOS
BETWEEN PREGNANCIES

Fig. 3-6: Egg and embryo growth in Strait of Georgia dogfish. (A) Changes in ovarian egg diameter prior to ovulation, (B) changes in embryo length prior to parturition, and (C) changes in volume of yolk during gestation.


EGG DIAMETER (cm)
4
3
2
1
0
OVULATION
(A)
EMBRYO LENGTH (cm)
25
20
15
10
5
0
PARTURITION
(B)
YOLK SAC VOLUME (cc)
30
20
10
0
TOTAL
EXTERNAL
INTERNAL
(C)
J A S O N D J F M A M J J A S O N D J F M
TIME (MONTH)

Strait of Georgia (Fig.3-2). Ages at 50% maturity sizes are 19 and 29 yr for males and females respectively (chapter 2). These length estimates at 50% maturity both exceed those of 72 cm for males and 92 cm for females noted earlier by Bonham et al. (1949) for waters off Washington State, U.S.A. The greater difference in the data for males may relate to the greater difficulty in determining the state of maturity, that is, microscope examination of testes sections as opposed to gross observation of uterine and ovarian contents. Though the size differences when 50% of stock reach maturity may result from different sample sizes or methods, they may also be reflections of different rates of maturation under the different environmental conditions of the Strait of Georgia and the Washington coast. However, another possibility exists. There was some indication in the examination of testes that smaller males mate earlier than larger ones (discussed later). Thus, biases in sampling time might influence determination of length when 50% are mature though this is unlikely in my determinations as data were collected regularly throughout the year. Bonham et al. (1949) did not indicate when their data were collected so no further comparison is possible. The modal length of mature males (Fig.3-4) was 85 cm achieved at 25 yr age (chapter 2). For mature females (Fig.3-3) the modal length was 100 cm at 35 yr age. Age was determined from the von Bertalanffy growth equations in chapter 2. Thus, males mature 15 cm shorter and 10 yr younger than females. Mean length and age data at various stages in the life history of dogfish are summarized in Table 3-2. Though ages in excess

Table 3-2: Mean length and age at various stages in the life history of spiny dogfish in the Strait of Georgia, B.C.

	Males		Females	
Growth stage	Length(cm)	Age(yr)[a]	Length(cm)	Age(yr)[a]
(1) Birth	26[b]	0	25[b]	0
(2) Shortest mature	72	15	76[c]	18
(3) 50% maturity	78.5	19	93.5[c]	29
(4) Mature mode	85	25	100	35
(5) Longest immature	93	40	118[c]	63
(6) Maximum size	103[b]	-	130[b]	-

[a] Calculated from von Bertalanffy growth equations in chapter 2.

[b] From chapter 2.

[c] From Ketchen (1972).

of 40 and 63 yr for males and females respectively are indicated, these are extrapolated beyond the 36 yr for males and 48 yr for females actually determined in chapter 2. However, Ketchen (1975) has determined dogfish ages for females as high as 64 yr by an independent method, thus my projections are plausible.

The mean number of female embryos per breeding female necessary to produce one breeding female at modal length of matures is estimated as 3.57 (Table 3-1). At modal length the number of survivors is 2.27 (Table 3-1), thus mortality from birth to age 35 yr for female dogfish is only 36%. In the absence of more accurate data, I assumed that numbers of mature males at modal length are equivalent to those of mature females. Thus, males would have a higher mortality rate as it acts over a shorter time period. These low rates of mortality are not unusual for a predator with few natural enemies. Assuming no intra-uterine mortality and a 50:50 sex ratio, the mean number of young produced per breeding female would be 7.14. This is approximately equivalent to the mean 7.3 embryos per breeding female observed in my total samples, but somewhat greater than the 6.2 embryos at modal length estimated by Ketchen (1972). His estimate did not take into consideration the greater contribution made by females larger than the mode. As indicated in Table 3-1, most embryos [$l_x m_x$] are produced by females from 35 to 37 years of age, rather than at modal age of matures.

Mating takes place between October and February. This is deduced from histological examination of testes and occurs between the time of maximum percentages of ripe sperm (E) and evacuated ampullae (F)(Fig.3-1). Shorter dogfish appeared to mate earlier than larger ones. When the data were segregated into three length groups, I observed maximum percentages of ripe sperm in males <80 cm in September, during October for those 80 to 90 cm, and in November for males >90 cm ($P<.05$). The time period from the maximum percentages of spermatocytes (A) to evacuated ampullae (F) is 1.2 yr (Fig.3-1). Considering that additional time is required to produce spermatogonia from the germ ridge and spermatocytes from spermatogonia, a spermatogenic cycle of close to two years is likely. However, two simultaneous waves of differential development are suggested since two stages of spermatogenesis separated by a band of degenerate tissue appear to occur at any one time. Thus, it seems likely that males have the capacity to mate each year.

For females (Fig.3-5), the appearance of "candles" between September and January signifies that mating has occurred. During this period females between pregnancies (parturition has occurred, but not ovulation) are also found; their proportions peak in December. Ketchen (1972) has estimated the period of mating of female dogfish as December to February, a somewhat shorter and later time than mine. My sampling was more frequent, which probably accounts for this difference, and suggests that dogfish mating occurs between October and January, and peaks in December.

The mature eggs are released from the ovary at a diameter of 4.0 ± 0.1 cm (mean ± 1 SD) after mating, fertilized in the shell gland, and encapsulated. A small number (1.1%) of large ovarian eggs are not released from the ovary and degenerate. The fertilized eggs remain in candles for approximately 4 months (50% levels, Fig.3-5). Around April, rather than in the fall as suggested by Lucas (1930), the candles rupture releasing embryos with large external yolk sacs into the uteri. Embryo growth in length from shortly after candle break-down to parturition (26 cm) is indicated in Fig.3-6B. During embryonic growth the external yolk sac contents are totally absorbed, but the internal yolk sac contents increase to a maximum of 5 cc at 24 cm length in September to October, 1.5 months prior to birth. For northwestern Atlantic dogfish, Wolf (1963) noted a similar mean maximum volume, but at an earlier stage of growth (20 cm), four months prior to birth. However, his data were based on very few samples, none of which were near or after the period of parturition. My data indicate some yolk still remains in the internal yolk sac for two months after parturition, and likely serves as a source of nourishment for the young during the onset of feeding. In this regard, pups (with small external yolk sacs) removed from the uterus were observed feeding on small pieces of salmon fingerlings the next day.

The period of parturition was indicated as September to January, with a mean of November (Fig.3-5). This is somewhat broader than the

October to December range of Ketchen (1972), and may be a reflection of my regular sampling program. Gestation extends from December of one year to November two years hence (50% levels), a period of 23 months.

Chapter 4

FOOD AND FEEDING

INTRODUCTION

Spiny dogfish have long been implicated by British Columbia fishermen as being a major exploiter of commercially important marine organisms. Few data have previously been available to either refute or substantiate these claims. This study was designed to assess the feeding habits of dogfish and thereby attempt to clarify this issue.

The usual method of determining the diet of fishes has been to identify the contents of a number of stomachs and determine the numbers or volume of each food type, or its frequency of occurrence in stomachs. Some studies of this type have also described food eaten at different times of the year or by different sizes of fish (Windell 1968). However, a food budget which considers seasonal variation in consumption and the relative biomass and intake requirements as related to size and sex would provide a more accurate measure of food consumption by dogfish. Several workers (Razum 1952; Chatwin and Forrester 1953; Bonham 1954) have attempted to provide a range of dietary data, but did not have large enough samples of different sizes and sexes of dogfish from each area and time of year for a representative picture. They also lacked data on the effect of availability to gear and gear selectivity on the observed diet and knowledge of rate of food consumption. I attempted to minimize these deficiencies by bringing together as many stomach samples as possible, collected with all types of gear. The data were converted, by reference to consumption, biomass, and metabolism studies, into mean annual consumption estimates of each food type per unit stock, and used to indicate possible impact of dogfish on species of importance to British Columbia commercial fisheries.

MATERIALS AND METHODS

Data on diet were obtained by examination of stomachs from 14,796 dogfish caught in British Columbia waters with a variety of gear during this study and over the past 30 years by staff of the Pacific Biological Station, Nanaimo, B.C. The numbers examined by size, sex, and season are presented in Table 4-1.

To make best use of the available data, stomach contents were recorded by the frequency of occurrence method. This involves determining the percentage frequency of each recognizable food type relative to the total number of occurrences of food types identified in all stomachs examined. To convert these data into a form more applicable to the prediction of total dogfish impact on individual prey species, occurrences of each food type were segregated by season into five distinct groups according to dogfish size and sex. The dogfish groups were defined on the basis of total lengths suggested by Ford (1921) and my trawl surveys as follows:

Table 4-1: Numbers of dogfish from British Columbia waters by size, sex, and season used in stomach content analysis. The percentage empty in each group is also indicated.

Size/Sex group	Length group (cm)	Season (months)				Total numbers	Total empty(%)
		Winter (JFM)	Spring (AMJ)	Summer (JAS)	Fall (OND)		
(A) Young	<46	97[a]	37	65	13	212	31.5
		233[b]	218	182	39	672	
		174[c]	224	86	24	508	
(B) Immatures	46 - 78	446	220	270	187	1123	32.2
		753	912	1175	643	3483	
		237	779	978	469	2463	
(C) Subadult ♀	79 - 93	279	162	96	237	774	37.9
		600	412	297	731	2040	
		254	252	218	471	1195	
(D) Mature ♂	>78	926	342	721	347	2336	36.9
		1767	1096	2556	904	6323	
		687	773	1874	521	3855	
(E) Mature ♀	>93	343	176	49	317	885	38.8
		918	416	146	798	2278	
		500	246	100	458	1304	
Total		2091	937	1201	1101	5330	36.0
		4271	3054	4356	3115	14796	
		1852	2274	3256	1943	9325	

[a] Number of dogfish with empty stomachs.

[b] Total number of dogfish examined.

[c] Number of occurrences of recognizable food. The stomach of each fish may contain more than one type of recognizable food plus unidentifiable animal remains and bottom materials.

(A) Young - males and females less than 46 cm which form a relatively coherent pelagic group.

(B) Immatures - males and females from 46 to 78 cm, separated mainly because of the distinctiveness of other groups.

(C) Subadult females - from 79 to 93 cm. Those whose length fell between the 50% maturity sizes of males and females as noted for the following groups.

(D) Mature males - above 78 cm. Those whose length exceeded that observed at the 50% maturity level established in chapter 3.

(E) Mature females - above 93 cm. Those whose length exceeded that observed at the 50% maturity level established by Ketchen (1972).

From the segregated occurrence data I developed an annual food budget for a unit stock, which constituted a summation of proportional consumption of individual food types by each of the dogfish groups after correction factors for seasonal variation in consumption, differential relative biomass and intake requirements are applied.

Seasonal variation in consumption was determined with a minimum of 12 to a maximum of 33 dogfish 60-111 cm length. These were taken off Nanaimo and maintained in a 30x15x10m deep netted enclosure in Departure Bay, B.C., from April, 1974, to March, 1975. They were allowed to feed voluntarily on herring suspended from a float line. Approximately 25% more herring than dogfish present were put out, and replaced every 2 or 3 days, as preliminary study indicated this to be an adequate rate of supply. Numbers and weight of dogfish present in the enclosure were checked monthly; approximately 33% of enclosure biomass was incorporated within mature female tissue. Consumption was recorded as daily weight of herring eaten per kg dogfish (Fig.4-1) under the assumption that herring lost to other sources was balanced by consumption of other organisms in the enclosure by dogfish. The data were highly variable and were smoothed by a moving average of fives to clarify the trend of greater consumption in summer than winter. Mean daily consumption, as derived from the total integrated area under the curve, was 1.3% of dogfish biomass. Relative consumption per season was derived from the integrated area under the curve for each season as a percentage of the total area (factor c in Table 4-2). The young and immature groups were assumed to follow the same feeding pattern as adults although they were largely unrepresented in the size group kept in the marine enclosure.

Intake requirements of dogfish groups, in terms of proportion of own weight consumed annually, were calculated from data on feeding of captive young, mean dailly consumption derived from the marine enclosure dogfish, and growth rate estimates in chapter 2.

Fig. 4-1: Variation in herring consumption over one year by dogfish held in a netted enclosure in Departure Bay, B.C. Each point is derived from a 5-point moving average. The dashed lines connecting points signify periods for which no records are available.

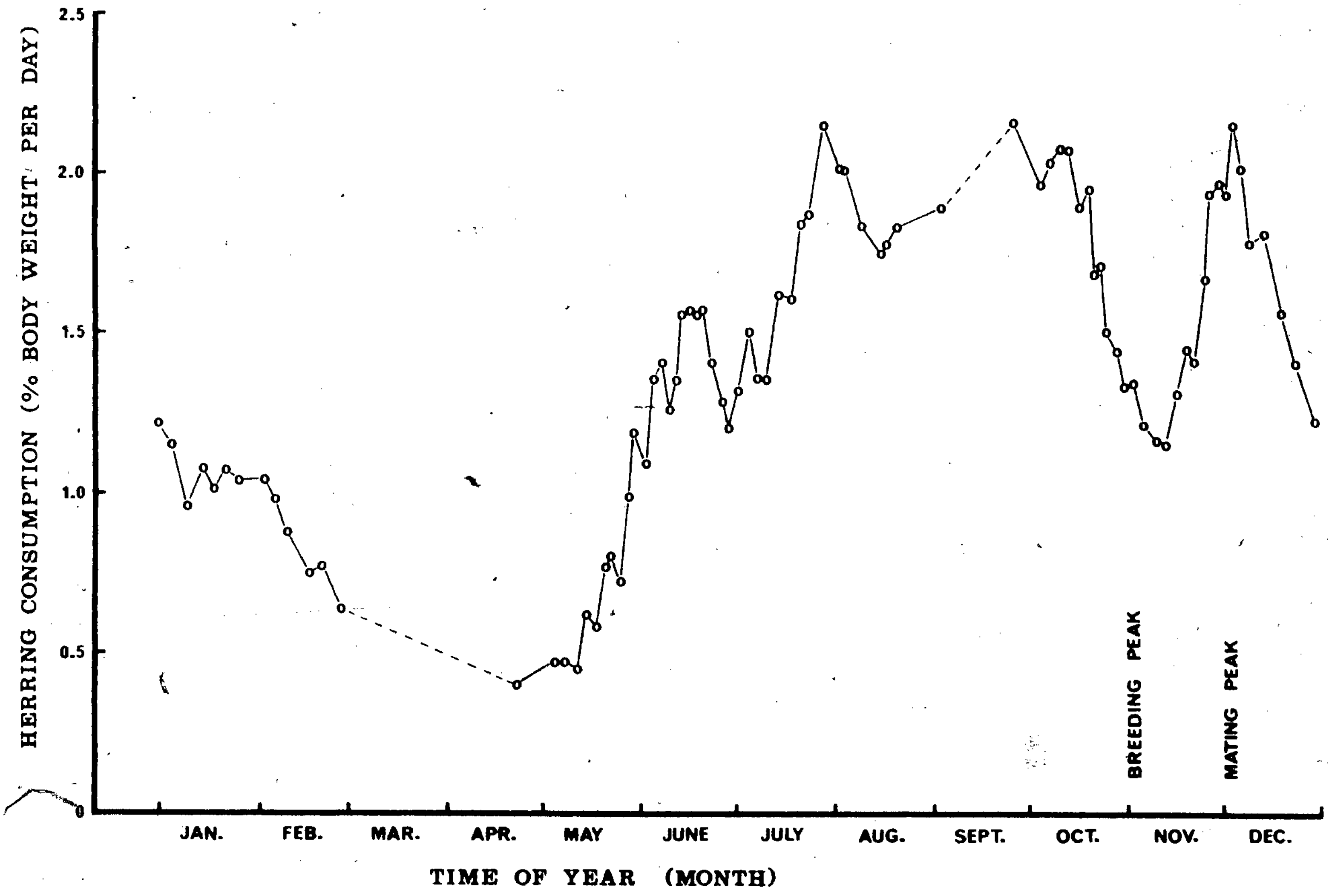

HERRING CONSUMPTION (% BODY WEIGHT PER DAY)
2.5
2.0
1.5
1.0
0.5
0
JAN.
FEB.
MAR.
APR.
MAY
JUNE
JULY
AUG.
SEPT.
OCT.
NOV.
DEC.
BREEDING PEAK
MATING PEAK
TIME OF YEAR (MONTH)

Table 4-2: Correction factors for application in dogfish food budget calculations derived by combining terms for biomass, metabolic intake, and consumption according to season, size, and sex. Each figure in the group-season matrix is the percentage of the total annual stock intake consumed by dogfish in that category, and is derived by multiplying the corresponding three factors together (axbxc; same as footnotes) and reducing the sum of all categories to 100%.

Size/Sex group	Season				Proportional biomass(%)[a]	Intake requirement[b]
	Winter	Spring	Summer	Fall		
Young	0.6	0.7	1.4	1.2	2.1	5.0
Immatures	2.0	2.2	4.3	3.8	10.4	3.2
Subadult ♀	4.3	4.8	9.3	8.3	26.9	2.7
Adult ♂	3.1	3.5	6.8	6.0	21.1	2.5
Adult ♀	6.0	6.8	13.2	11.7	39.5	2.6
Relative consumption(%)[c]	16	18	35	31	-	-

[a] Relative biomass of groups in unit stock, as derived from mean numbers and weight per size (Fig.4-3).

[b] Annual intake requirements (number of times own mean weight consumed) for groups as derived from consumption and growth studies. Mean annual intake equals 2.719 times unit stock weight and is computed by the formula $\Sigma(axb/100)$.

[c] Seasonal consumption means derived from marine enclosure data (Fig.4-1). Each value represents the integrated area under the curve for that season as a percentage of the total integrated area. The feeding patterns of all dogfish groups were assumed to be similar.

Consumption rate estimates for young were derived by maintaining five pups (taken from full term females caught by set-line) for up to 1.5 years in a 0.6x1.2x0.9 m deep indoor fibreglass tank in which mean temperature was close to 10 C. They were allowed to feed voluntarily on pieces of sockeye salmon fingerlings supplied daily. Dates of ingestions and mean weight consumed were recorded. Approximately 2.5 gm per feeding were consumed just after birth increasing to 13 gm by one year of age. A mean of 5.7 gm was ingested every 2.6 days over the first year of life. Mean initial weight of 55.2 gm increased by 180% during this period, roughly 2.7 times the 66% weight increase normally encountered during the first year of life in the wild (chapter 2). However, there was no mean gain or loss in weight among dogfish in the marine enclosure. Thus, they were likely at a subsistence level of consumption. Applying a food conversion ratio of 12% [180%(55.2)/5.7(365/2.6)], derived from increase in weight of captive young relative to their total intake during the first year of life, to the mean daily 1.3% body weight intake in the enclosure, the annual consumption by dogfish would be about 1.8 times $[(1+0.013(0.12))^{365}]$ their biomass. In the wild, weight increases 33.4% per year for the young decreasing to 3.1% for mature individuals (chapter 2). With a 12% food conversion ratio and assuming a 25% allowance for increase in activity for capturing prey, the annual intake requirement would be about five times [1.8+25%(1.8)+33.4(1/0.12)/100] body weight for young decreasing to about half that for mature dogfish (factor b in Table 4-2).

As an independent check on annual intake estimates, stomach clearance rates were estimated by force-feeding 75 dogfish (70-107 cm length caught by set-line off Nanaimo) with whole herring or salmon (17-27 cm length) during mid-June through August, 1974. Up to 6 dogfish were retained in a 2 m diameter x 1 m deep fibreglass tank at about 10 C for one week prior to force-feeding. At specific times after feeding the dogfish were killed and stomach contents removed. Twenty-five dogfish had empty stomachs. The solid materials in all others were weighed after excess moisture had been removed; the difference in weight of solids before and after feeding was attributed to digestion. Stomach clearance rates were subsequently applied to stomach capacity data for dogfish of similar size to estimate maximum annual consumption. Stomach volumes (Fig.4-2) were determined by removing stomachs just after the animals were killed, tying off the pylorus, and filling the unsupported stomach with water to its junction with the esophagus (papilla region). No allowance was made for possible unnatural stretching of stomachs and no data were available for animals 30 to 65 cm.

Dogfish biomass estimates were calculated from mean weight and numbers derived from survivorship curves (Fig.4-3; based on chapter 3 data) and weight-length data in chapter 2. At modal length (100 cm) one breeding female produces 3.57 female pups annually (chapter 3). Since gestation takes 2 yr, only 1.79 per year are produced per mature

Fig. 4-2: Relationship of stomach volume to body length of dogfish from the Strait of Georgia, B.C. Curve fitted by eye.

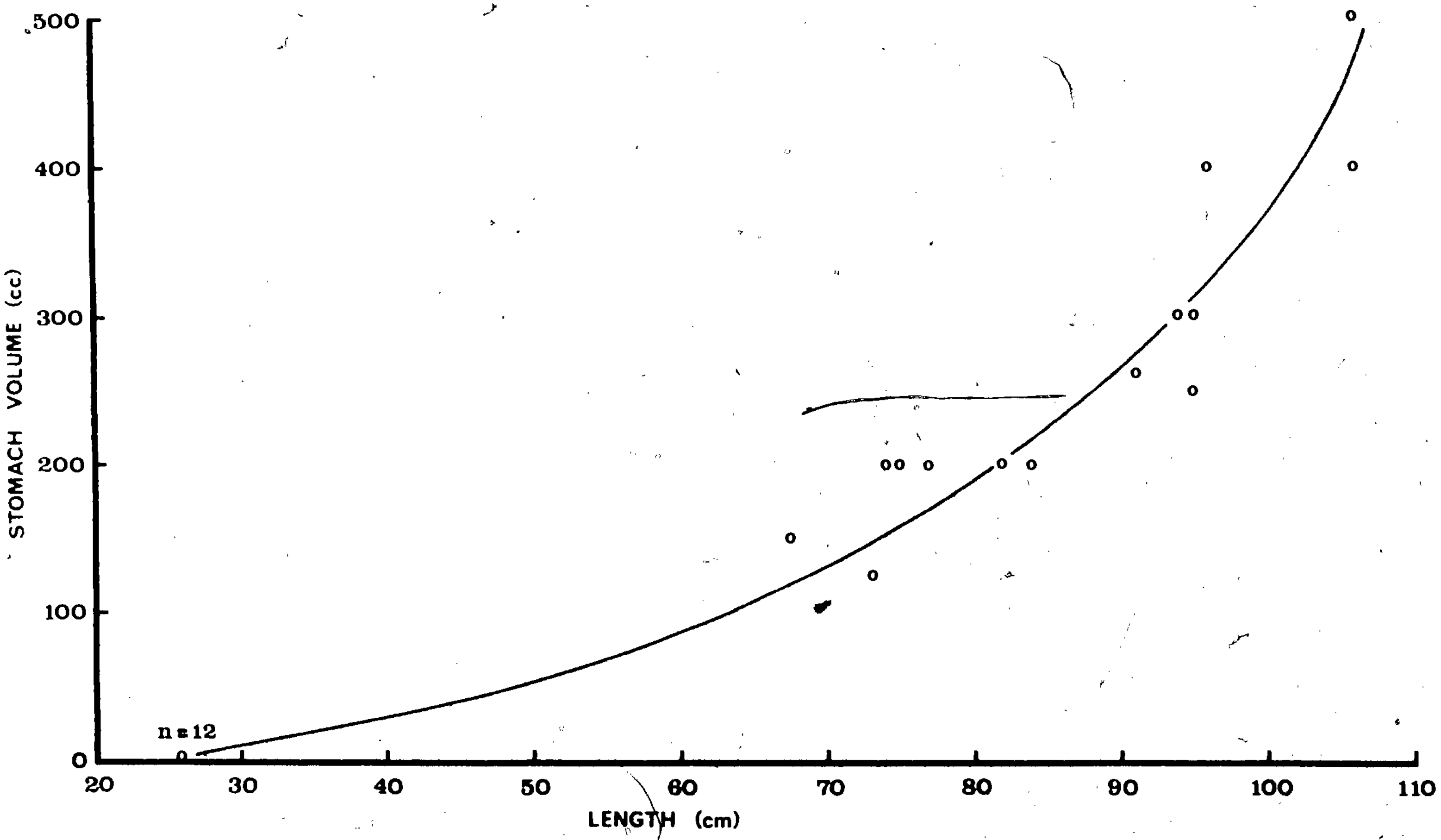
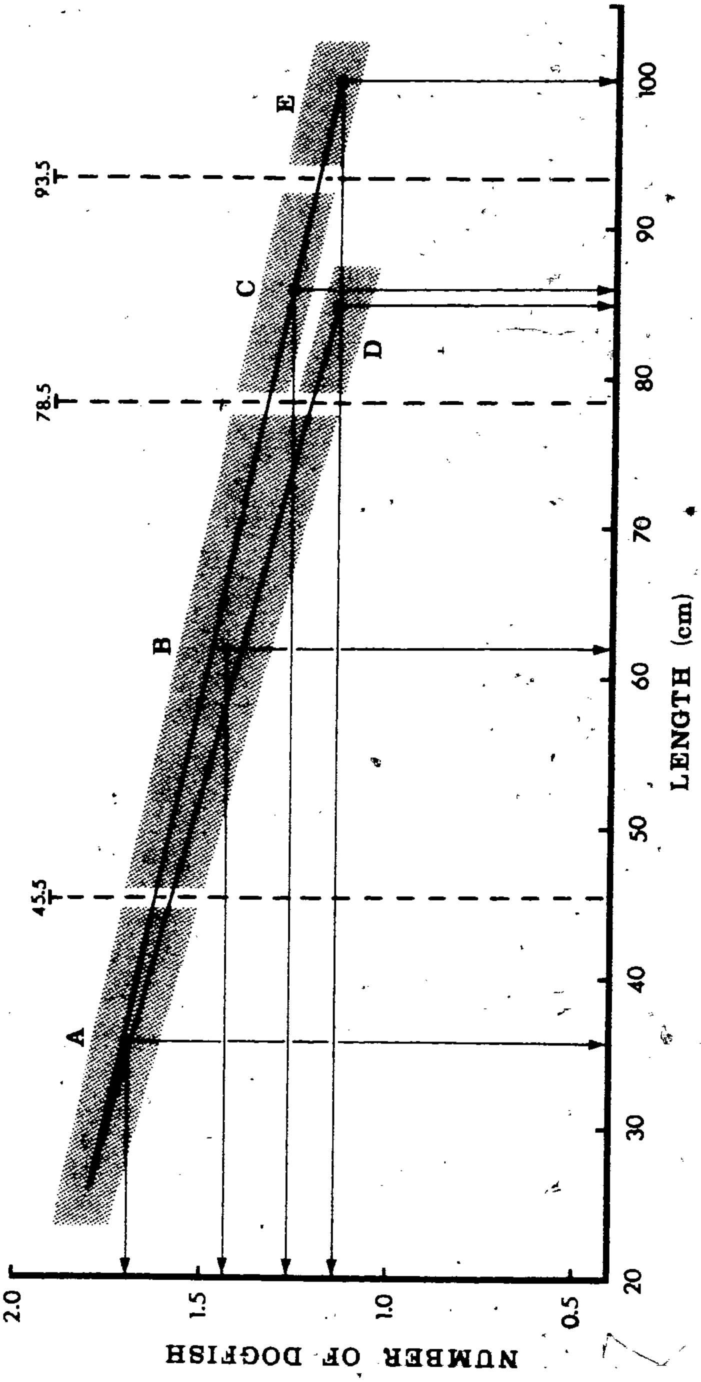

STOMACH VOLUME (cc)
500
400
300
200
100
0
20
30
40
50
60
70
80
90
100
110
LENGTH (cm)
n = 12

Fig. 4-3: Assumed relative survivorship curves for dogfish in British Columbia waters based on number surviving per mature female. Shaded areas delineate apparently distinct sex and size groups with the arrows noting their respective mean lengths and numbers. Curves end at modal length of matures, but in reality decrease rapidly beyond this length to zero at 103 and 130 cm for males and females respectively. A = young, B = immatures, C = subadult females, D = mature males, and E = mature females. Based on data in chapter 3.


NUMBER OF DOGFISH
2.0
1.5
1.0
0.5
LENGTH (cm)
20
30
40
50
60
70
80
90
100
A
B
C
D
E
45.5
78.5
93.5
T
T
T

female, but at modal length only 88% are mature (Ketchen 1972). Therefore, a survivorship curve for females, if the number mature at modal length is equated to one and a constant mortality rate is assumed, originates with 1.79 pups at birth (26 cm) and extends to 1.14 individuals (1/0.88) at the modal length of matures (100 cm). Males have a modal length of matures at 85 cm, but with only 87% mature at this length (chapter 3). Assuming a 50:50 sex ratio and that their mature numbers at modal length are similar to those of mature females at modal length, a survivorship curve for males can also be constructed originating at 1.79 pups at birth and extending to 1.15 individuals (1/0.87) at 85 cm. When these curves (Fig.4-3) are subdivided according to size, and mean numbers and lengths are derived for each dogfish group, biomass estimates can be calculated. A greater biomass in the larger size groups is evident in these data (factor a in Table 4-2).

The correction factors are combined on a relative basis in Table 4-2 in order to facilitate food budget calculations. These involved multiplying the occurrence percentage for each food type, when segregated according to dogfish size, sex, and season of capture, by the corresponding combined correction factor, and summing the products for all groups. For example, calculations to determine the relative consumption of euphausids by dogfish in British Columbia waters are shown in Table 4-3. The number of euphausid occurrences for each category of size, sex, and season are converted to a percentage of all

Table 4-3: Sample calculations of food budget and occurrence percentage for dogfish consumption of euphausids in British Columbia waters. The top figure in each category (a) is the actual number of occurrences of stomachs containing euphausids for that season, size, and sex category. The middle figure (b) is the percentage of euphausid occurrences from among all occurrences of recognizable food within the category. The bottom figure (c) is the product of this percentage (b) and its corresponding correction factor from Table 4-2. Annual consumption is derived from correction for seasonal variation only (factor c in Table 4-2), in order to indicate variation in consumption among groups.

Size/Sex Group	Season				Annual Consumption(%)
	Winter	Spring	Summer	Fall	
Young	77[a] 44.2[b] 0.265[c]	77 34.4 0.241	51 59.2 0.829	9 37.5 0.450	45.6
Immatures	20 8.4 0.168	268 34.5 0.759	247 25.3 1.088	55 11.7 0.445	20.0
Subadult ♀	2 0.8 0.034	78 30.9 1.483	45 20.5 1.907	23 4.9 0.407	14.3
Adult ♂	22 3.2 0.099	231 29.8 1.043	128 6.8 0.462	86 16.5 0.990	13.4
Adult ♀	1 0.2 0.012	23 9.4 0.639	10 10.0 1.320	9 2.0 0.234	5.8

Calculations for:

(1) Occurrence percentage = $\Sigma(a)(100)/\text{total occurrences}$

$= 1462(100)/9325 = 15.68\%$.

(2) Food budget = $\Sigma(c) = 12.87\%$.

food type occurrences for that category and multiplied by the corresponding combined correction factor in Table 4-2. The resultant percentages for all categories are summed and indicate that euphausids constitute 12.87% of total stock diet. In comparison, the occurrence percentage of euphausids among all data is 15.68%, roughly 22% greater.

To convert the food budget percentages to proportional annual consumption per unit stock, or that percentage of its own weight that a unit stock annually consumes of any individual food type, the percentages were multiplied by 2.719 (the mean annual intake requirement of the total stock in terms of number of times own weight consumed) which was derived by weighting the intake requirement correction factor for the different dogfish groups by the corresponding differential biomass factor (Table 4-2). Absolute quantities of prey consumed are calculated by multiplying these data by 0.5 million metric tons, a total regional dogfish biomass estimate derived from Shepard and Stevenson (1956).

RESULTS

Empty stomachs were found in 36.0% of dogfish examined (Table 4-1). The monthly percentage of those with food in their stomachs shows a winter minimum and a summer maximum (Fig.4-4). The 9466 with food in their stomachs contained a mean of 1.16 different types of

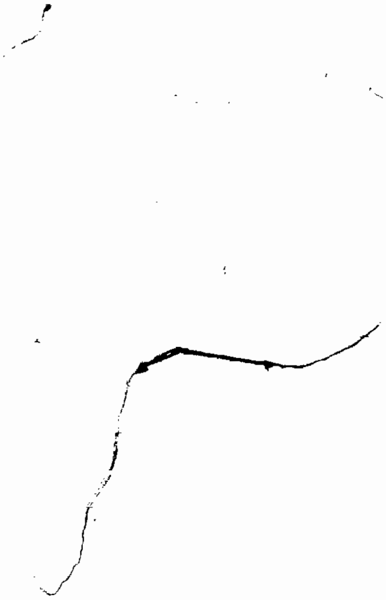
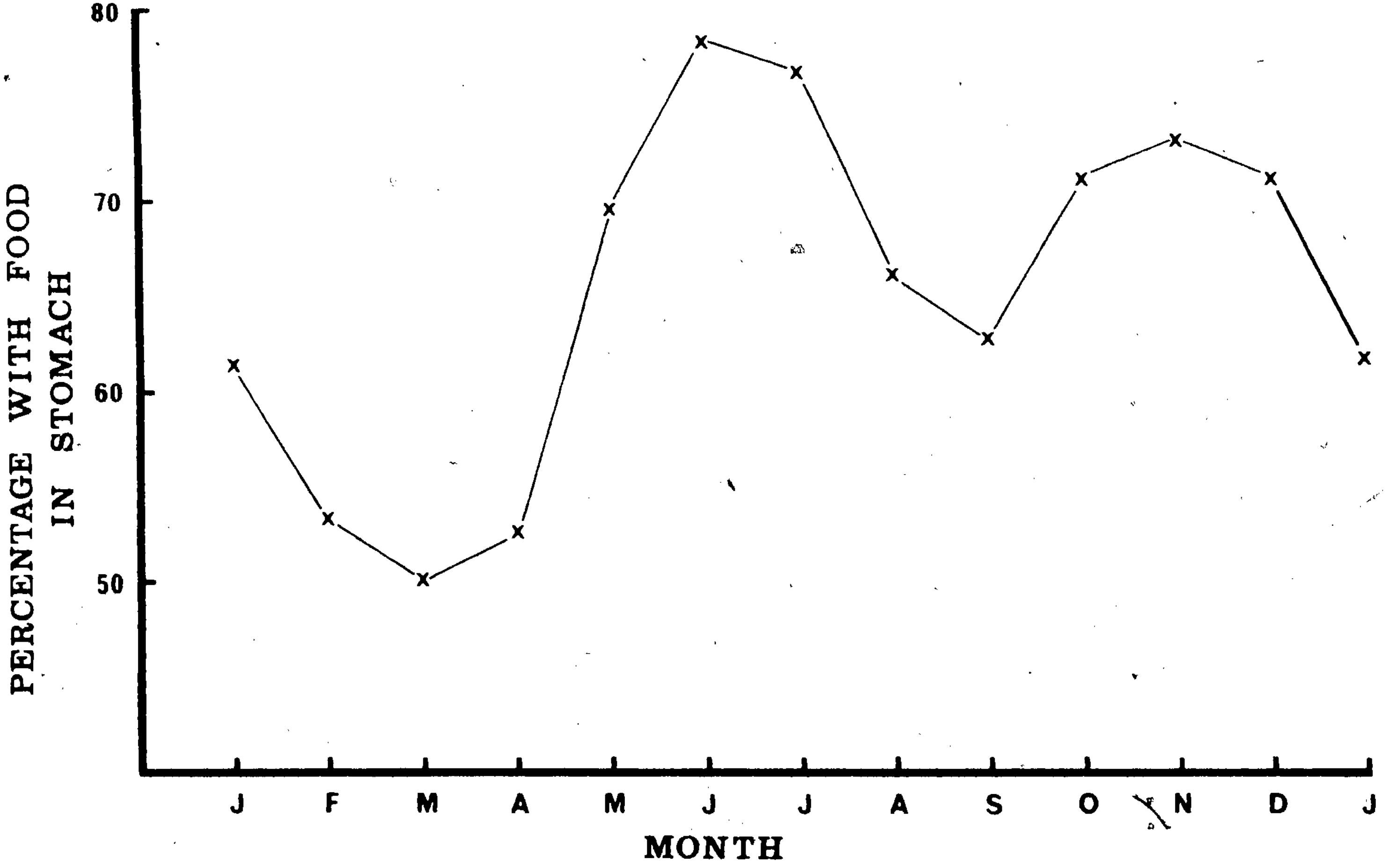


Fig. 4-4: Monthly variation in number of dogfish in British Columbia waters with food in stomach at time of capture. Curve smoothed by moving average of threes to clarify trend.


PERCENTAGE WITH FOOD IN STOMACH
80
70
60
50
J
F
M
A
M
J
J
A
S
O
N
D
J
MONTH

food organisms (a total of 10,983 occurrences). Recognizable food types constituted 9325 occurrences while the remainder consisted of bottom materials (such as mud, stones, and plant material) 11.6% and unidentifiable animal remains 3.5%.

The food budget percentages derived from the segregated occurrence data are shown in Table 4-4 in comparison to the occurrence percentages from among all recognizable food data. To indicate differences among dogfish size and sex groups, the mean annual consumption of food types by these groups individually are also indicated. These data are corrected for seasonal variation in consumption only, as noted in Table 4-3 for euphausids. The monthly variations in the number of occurrences of fishes and invertebrates consumed by different sizes and sexes of dogfish are shown in Fig.4-5. Pattern irregularities for the smaller sizes during the latter part of the year may be due to small sample sizes (Table 4-1). This study indicates the major dietary components of British Columbia dogfish to be 55% teleosts, 35% crustaceans, and 5% molluscs (Table 4-4). Herring is indicated as the single most important food species when the food budget percentages in the diet of dogfish are ranked (Table 4-5). Four individual species (herring, shrimp, hake, and eulachon) constitute over 42% of the diet, while salmon is less than 0.3%.

Stomach clearance rates of dogfish, as a check on intake requirements, were found to be independent of the size, sex, duration

Table 4-4: Mean annual percentage consumption of food types according to size and sex of dogfish in British Columbia waters. The resultant food budget is compared to the occurrence percentages from among all data. Only items with greater than 1% in at least one dogfish group are recorded. Food category totals are shown in brackets.

Recognizable food	Young (%)	Immature (%)	Subadult ♀ (%)	Mature ♂(%)	Mature ♀ (%)	Food budget(%)	Occurrence (%)
Plankton	(10.1)	(13.3)	(12.7)	(10.4)	(4.4)	(9.09)	(10.88)
Ctenophora:							
Combjelly (Pleurobrachia sp.)	(1.7)	(1.7)	(2.3)	(2.8)	(2.2)	(2.26)	(2.34)
Coelenterata:	(0.8)	(0.7)	(2.9)	(0.4)	(0.5)	(1.15)	(0.90)
Jellyfish (C. Scyphozoa)[a]	0.8	0.7	2.7	0.4	0.5	1.10	0.87
Mollusca:	(4.8)	(3.3)	(5.6)	(2.9)	(5.4)	(4.69)	(3.54)
Octopus (Octopus sp.)	0.1	1.6	4.3	2.0	3.0	2.87	2.14
Squid (Loligo sp.)	4.7	1.5	1.3	0.7	2.0	1.61	1.29
Annelida:							
Worm (O. Polychaeta)	(5.2)	(2.0)	(0.6)	(1.0)	(1.1)	(1.22)	(1.63)
Crustacea:	(60.4)	(33.9)	(28.2)	(27.3)	(22.4)	(27.78)	(31.02)
Amphipod (O. Amphipoda)	10.0	0.8	-	0.4	-	0.57*[b]	1.47
Crab (T. Brachyura)	-	2.2	6.5	2.3	11.2	6.68	3.72
Euphausid (O. Euphausiacea)	45.6	20.0	14.3	13.4	5.8	12.87	15.68
Shrimp (Pandalus sp.)	4.8	10.5	7.3	11.1	5.3	7.57	9.89
Echinodermata:	(-)	(0.4)	(0.4)	(0.3)	(0.2)	(0.30)	(0.41)
Unident. invertebrate	(0.8)	(3.2)	(2.6)	(3.3)	(2.9)	(2.85)	(2.96)
Cyclostomata:	(-)	(0.2)	(0.1)	(-)	(-)	(0.05)	(0.06)
Elasmobranchii:	(-)	(0.2)	(2.0)	(0.4)	(3.6)	(1.99)**	(0.89)
Ratfish (Hydrolagus sp.)	-	0.1	1.4	0.3	3.2	1.65**	0.69
Teleostei:	(16.2)	(41.1)	(42.6)	(51.2)	(57.3)	(48.62)	(45.37)
Herring (Clupea sp.)	0.5	10.6	10.3	23.0	15.6	14.42	16.33
Eulachon (Thaleichthys sp.)	13.4	10.2	2.6	3.0	1.6	3.65	3.23
Hake (Merluccius sp.)	-	1.7	5.0	0.9	7.3	4.48	2.68
Cod (F. Gadidae)	-	0.4	0.1	0.7	1.8	0.89	0.69
Flatfish (O. Heterosomata)	-	0.7	3.4	0.9	7.2	3.89**	1.64
Seaperch (F. Embiotocidae)	-	0.3	1.0	0.3	1.8	1.04**	0.38
Rockfish (F. Scorpaenidae)	-	0.4	1.0	0.7	1.4	0.98	0.60
Sandlance (Ammodytes sp.)	-	2.2	0.5	2.3	0.7	1.11	1.60
Unident. Teleostei	1.9	13.2	16.7	18.0	18.2	16.52	16.75

[a] In nomenclature C=class, O=order, T=tribe, and F=family.

[b] In a ratio of budget to occurrence percentages, *=less than halved and **=more than doubled from occurrence method.

Fig. 4-5: Monthly consumption of invertebrates and fishes by dogfish in British Columbia waters in relation to size and sex. A 3-point moving average is applied to months and 10 cm length intervals to clarify data trends.

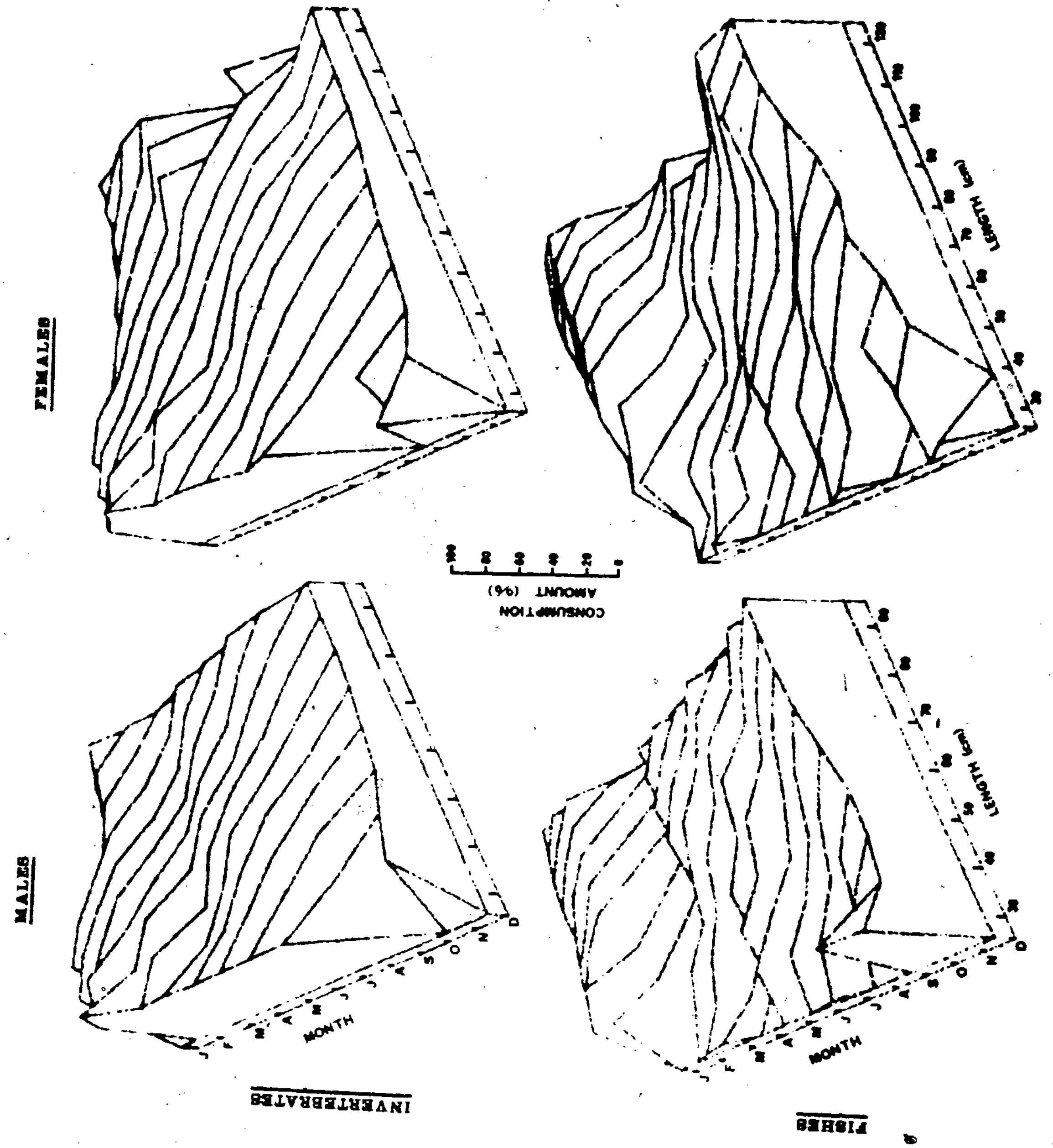

FEMALES
MALES
INVERTEBRATES
FISHES
CONSUMPTION AMOUNT (%)
0
20
40
60
80
100
LENGTH (cm)
30
40
50
60
70
80
90
100
110
120
MONTH
J
F
M
A
M
J
J
A
S
O
N
D

Table 4-5: Individual food types in the food budget of dogfish in British Columbia waters ranked from highest to lowest. Annual consumption per unit stock is derived by multiplying these data by the proportional mean annual intake requirement of the stock as a whole (2.719 from Table 4-2).

Position	Food Item	Diet amount (%)[a]	Cummulative total (%)	Annual consumption per unit stock (%)[b]
1	Herring	21.84	21.84	59.4
2	Euphausid	13.63	35.47	37.1
3	Plankton	9.65	45.12	26.2
4	Shrimp	8.03	53.15	21.8
5	Crab	7.09	60.24	19.3
6	Hake	6.79	67.03	18.5
7	Flatfish	5.89	72.92	16.0
8	Eulachon	5.53	78.45	15.0
9	Octopus	3.05	81.50	8.3
10	Combjelly	2.40	83.90	6.5
11	Squid	1.71	85.61	4.6
12	Sandlance	1.68	87.29	4.6
13	Ratfish	1.65	88.94	4.5
14	Seaperch	1.58	90.52	4.3
15	Rockfish	1.48	92.00	4.0
16	Cod	1.35	93.35	3.7
17	Polychaete	1.29	94.64	3.5
18	Jellyfish	1.17	95.81	3.2
19	Eelpout	0.67	96.48	1.8
20	Amphipod	0.60	97.08	1.6
21	Sculpin	0.35	97.43	1.0
22	Salmon	0.29	97.72	0.8
23	Dogfish[c]	0.28	98.00	0.8
24	Sablefish	0.27	98.27	0.7
25	Sea cucumber	0.25	98.52	0.7
26	Bivalve	0.22	98.74	0.6
27	Midshipman	0.15	98.89	0.4
28	Blenny	0.15	99.04	0.4
29	Prawn	0.14	99.18	0.4
30	Other	0.82	100.00	2.2

[a] Unidentified invertebrate and fish percentages prorated over respective groups.

[b] Percentage of its own weight that a unit stock annually consumes of any individual food type.

[c] Not likely representative of natural consumption as it was observed that dissected dogfish thrown overboard soon appeared in stomachs of dogfish caught in subsequent trawls.

of captivity prior to testing, time of year, and food species and condition (frozen storage time), although size of the food item had a significant influence (Fig.4-6). For herring, a regression equation describing daily percentage digestion (D) on prey weight (W) was:

$$D(\%) = 30.7 - 0.088W \text{ (gm)}$$

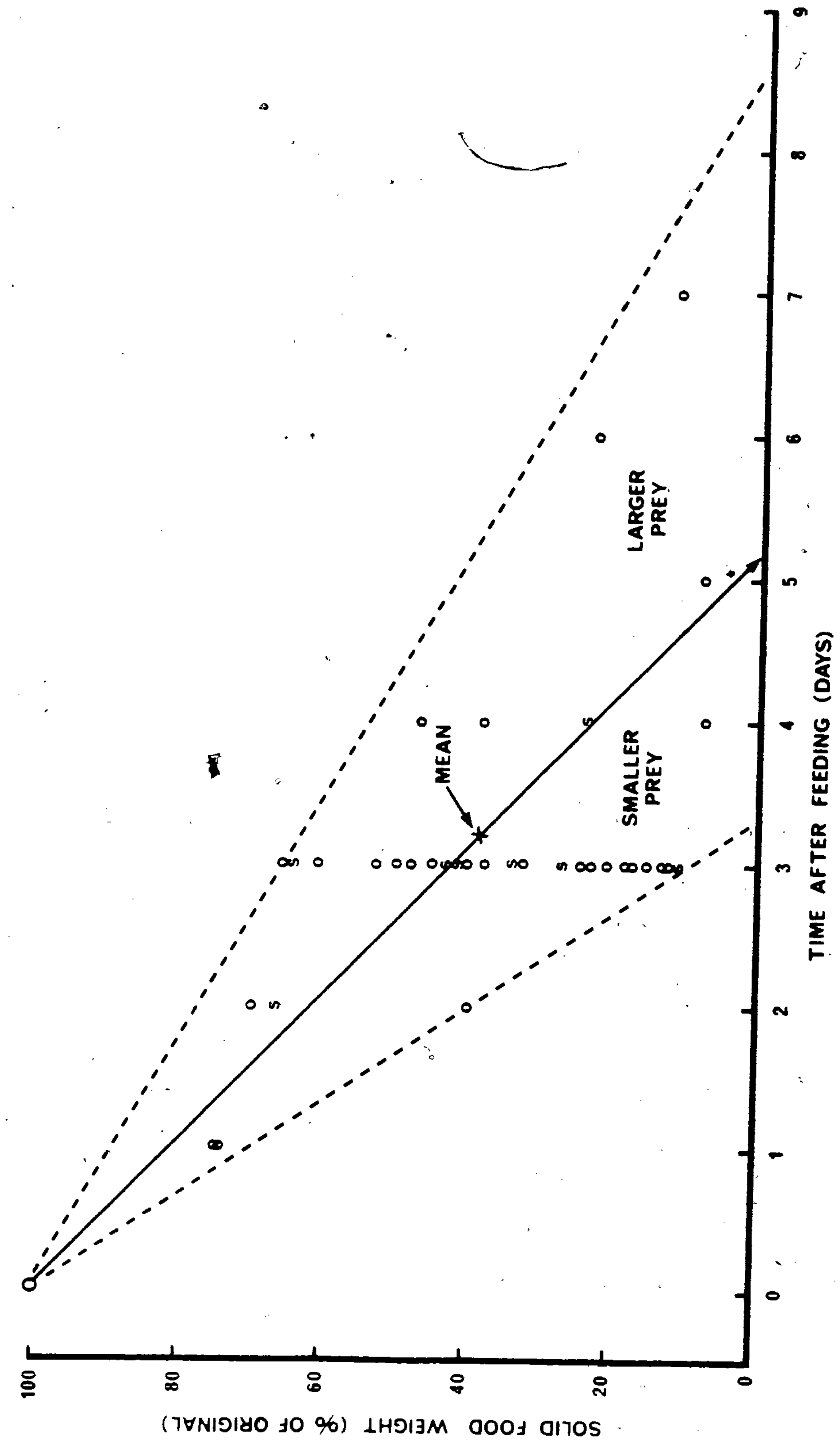
$$(p < 0.05;\ r = 0.61;\ n = 27)$$

Mean herring weight was 120.3 gm and required a mean of 3.2 days to reduce this amount to 38.0% of its original weight. Plotting this point on Fig.4-6 and extending a line linearly from the point of origin at 100% and zero days through the mean point to the abscissa, indicated a stomach residence time of 5.16 days to completely break down herring of this original weight.

DISCUSSION

In this work I attempted to put together a food budget (Table 4-4) for a unit stock of spiny dogfish to provide a basis for calculating impact on prey species. The data indicated that euphausids are the major food of young and immature groups at all times of the year (Table 4-3,4), and are important in the diet of larger dogfish during the spring and summer months. The diet of smaller dogfish is further supplemented by plankton, amphipods, and small fishes such as eulachon and herring. By the time dogfish reach

Fig. 4-6: Digestion rate of force-fed herring (o) in stomachs of dogfish from the Strait of Georgia, B.C. Mean herring weight was 120.3 gm, requiring a calculated 5.16 days to be completely reduced to the fluid state. Data on digestion of sockeye salmon (s) are superimposed.


SOLID FOOD WEIGHT (% OF ORIGINAL)
100
80
60
40
20
0
TIME AFTER FEEDING (DAYS)
0
1
2
3
4
5
6
7
8
9
MEAN
SMALLER PREY
LARGER PREY
S

78 cm, herring rivals euphausids in dietary importance and soon thereafter become the major food, particularly in fall and winter months. Dietary diversity also increases with increased dogfish size, possibly reflecting the greater ability of larger individuals to pursue and catch prey. For the total stock, fishes and invertebrates are consumed in approximately equal percentages. However, the dietary importance of each varies seasonally with dogfish size. As the animal grows, the primary dietary component shifts from invertebrates towards fishes (Fig.4-5). For larger animals, the greatest percentage of the diet of both sexes consists of fishes in winter and invertebrates in summer. On average over 80% of the food was pelagic. Food of smaller dogfish was obtained to a greater degree from the pelagic zone (86%) than that of mature males (78%) or mature females (70%) suggesting that mature dogfish are more demersal, an observation verified by trawl surveys (Jones 1974).

Among the characteristics used to derive the food budget was seasonal variation in consumption as derived from the marine enclosure data (Fig.4-1). Food intake was greatest during the summer and early autumn and least in late winter and early spring, a pattern observed for other sharks by Clark (1963). The data in Fig.4-1 indicate that dogfish consume twice as much in summer as in winter. The decrease in October-November corresponds to the breeding season when the mature females move inshore, release their pups, and apparently cease feeding (Springer 1967). The difference between the mean maximum and minimum consumption levels during this period (Fig.4-1) corresponds to a 37% decrease in the daily rate of consumption. This closely matches the proportional weight of mature females (33%) in the netted enclosure which might be expected not to feed during the breeding period, and hence reduce relative consumption accordingly.

The budget was also corrected for the proportional intake requirements of the different size groups. Brett and Blackburn (in press) found that at a routine level of activity (slow cruising such as observed in the marine enclosure) a large dogfish utilized sufficient oxygen to require an annual food intake of 1.8 times its body weight, a value similar to that determined from enclosure data. For young kept in captivity (this study), the annual intake equalled 5.4 times [5.7(365/2.6)/55.2(2.7)] their initial weight after compensation for 2.7 times greater growth rate than in the wild. This estimate was, as expected, slightly greater than the 5.0 found in Table 4-2 for the young dogfish group which would have a lower metabolic rate. To check intake requirements further, stomach clearance rates were examined in conjunction with the variation in percentages of empty stomachs among dogfish groups (Table 4-1). When the variation in percentages of dogfish with food in their stomachs are derived from empty stomach data (Fig.4-4) and compared with the variation in consumption by dogfish in the marine enclosure (Fig.4-1), it will be noted that the minima and maxima occur at approximately the same periods of late winter and summer respectively given a degree of time lag possibly relating to differential environmental influence. Since all contents in any one stomach were normally in the same state of digestion when examined in the field, and force-fed herring were always found to be retained in the stomach until fully broken down (this study; Hogben 1967), it is suggested that stomach residence time (the total food break-down period) is inversely related to the variation in proportions of empty stomachs (representing the time between which food material has left the stomach and subsequent feeding). The mean percentage of empty stomachs (Table 4-1) increased from 31% for the young to 39% in the mature females. The lower percentages probably indicate a shorter stomach residence time in as much as smaller food organisms eaten by smaller dogfish likely require less time to digest than larger organisms. When the proportion of empty stomachs and rate of digestion as a function of size are known, it is possible to calculate the annual food intake. Mature males of mean length 85 cm had a mean weight of 2.15 kg and 36.9% empty stomachs (Table 4-1). It is assumed they would feed for 230 days [(1-0.369)365] of the year. With a digestion rate of 23.3 gm [120.3/5.16] per day as derived from mean herring weight and total digestion time (Fig.4-6), they would require an annual consumption of 2.5 times [(230x0.0233)/2.15] their weight which agrees with the estimate in Table 4-2. In this instance the stomach capacity of 85 cm dogfish would be 223 cc (Fig.4-2) which equals 234 gm of herring (sp.gr. 1.044). Thus, mature male dogfish would take 10 days (234/23.3) to digest a full stomach of herring, take 16 days

[10/(1-0.369)] between feedings, and feed only 23 times (365/16) per year. This latter figure is minimal, as a dogfish may not completely fill its stomach on each feeding or it may eat smaller organisms at certain times which may require less time to break down. Holden (1966) estimated 40 feedings per year. However, he did not specify the size range sampled. If they were generally smaller dogfish they would have higher metabolic rates and require a proportionally greater food intake. For other species of sharks, Clark (1963) has estimated an annual intake of from 2 to 5 times body weight, being greater for the smaller sizes. Though Brett and Blackburn (in press) suggested an annual intake of five times body weight for adults, their growth rate assumptions were considerably in excess of those indicated by my data.

Another factor used in calculating the stock food budget was the relative biomass of the different sex and size groups as determined from the survivorship curves of Fig.4-3. They imply a constant though greater mortality rate of males than females and a greater biomass of females than males. However, calculations indicated that if the survivorship curves were more convex or concave there would be little change in the relative biomass proportions noted in Table 4-2 for these groups.

A comparison of the food budget results with the occurrence percentages from among all data (Table 4-4) indicated that differences were as high as three-fold, with the budget calculations yielding a mean consumption value 31% greater. Though my approach is believed to provide more accurate estimates of dogfish diet and consumption rates than the uncorrected occurrence percentages from among the total data, the following possible sources of bias should be considered:

(1) The frequency of occurrence method used assumes that occurrence percentages accurately reflect proportional biomass intake of individual food types. Since most stomachs contained only one food type (mean 1.16) and were often largely full, this bias is reduced though still of primary consequence when interpreting my results.

(2) The occurrence method also assumes that various food types are equally digestible. In this work I found that herring and salmon of the same size were digested at the same rate. In addition, Windell (1967) found that similar-sized bluegill sunfish (Lepomis macrochirus) digested equal quantities of oligochaetes, arthropods, and fishes at the same rate. However, though dogfish food types may be digested at the same rate, they may reach unrecognizable stages at different times, thus resulting in higher proportions of soft-bodied types like ctenophores and coelenterates in the unidentifiable classification than other foods, and thus under-rating their actual dietary proportions. Similarly, other species have hard parts which are difficult to impossible to digest, such as octopus and squid beaks, and hence identification long after consumption is still possible. This source of bias is unaccounted for.

(3) My data further arise from opportunistic sampling in which many collectors took part. Thus, biases due to vessel purpose, gear selection, and differing individual ability to classify food species may exist. However, the multiplicity of samples collected over many years may have compensated for this error.

Bearing in mind the possible influence of the sources of error noted above, the annual consumption of commercial fisheries species can be calculated from the annual consumption per unit stock figures (Table 4-5) when dogfish biomass is known. Assuming that dogfish in British Columbia waters have now returned to their pre-World War II level of abundance, their biomass would approximate 0.5 million metric tons (Shepard and Stevenson 1956). Dogfish consumption of commercial species (A) based on this estimate is indicated in Table 4-6 in comparison to the 1974 commercial catch (B; Anonymous 1975). Although the high A/B ratio for shrimp and prawn may reflect low market demand for these species, this probably would not apply to major fisheries. Among the major commercial species, dogfish are estimated to have consumed 6.7 times as much herring and 0.6 times as much salmon. Though these figures certainly dispell the myth of the large consumption of salmon by dogfish, it cannot be denied that due to their opportunistic nature they will still eat salmon caught by line or net, and by so doing, waste fishing time and possibly destroy gear. Of more importance, however, is their effect on the herring fishery. Though they also destroy herring gear and waste fishing

Table 4-6: Estimated annual consumption of species of importance to commercial fisheries compared to 1974 Canadian catch records for British Columbia waters. This is calculated from an assumed dogfish stock level of 0.5 million metric tons applied to the annual consumption per unit stock figures of Table 4-5.

Species harvested[a]	(A) Dogfish consumption (1000's metric tons)	(B) 1974 Commercial catch (Anonymous 1975) (1000's metric tons)	Ratio A/B
Shrimp	109.0	1.17	93.2
Prawn	2.0	0.03	66.7
Crab[b]	48.3	1.14	42.4
Flatfish	80.0	7.78	10.3
Sablefish	3.5	0.34	10.3
Rockfish	20.0	2.68	7.46
Herring	297.0	44.66	6.65
Grey cod[c]	2.8	8.13	0.34
Salmon[d]	4.0	63.94	0.06

[a] Ranked according to A/B ratio from highest to lowest.

[b] Commercial Dungeness crabs assumed 50% of total.

[c] Grey cod approximately 15% of Cod (F. Gadidae) group.

[d] Includes sport fishery catch (approximately 1.5% by weight).

time, their calculated annual consumption of practically 300,000 metric tons of primarily adult herring must significantly reduce possible commercial catches and is considerably in excess of even record commercial herring catches off the British Columbia coast. A more recent estimate of British Columbia dogfish biomass by W.E. Johnson (personal communication) of the Pacific Biological Station is 0.39 million metric tons. This would indicate an A/B ratio for herring of 5.2; consumption still considerably in excess of commercial catch. With an adult herring stock level of 3.5 million metric tons (ibid) and assuming a further 50% biomass for immatures, total British Columbia herring biomass approximates 0.53 million metric tons. At the dogfish stock size suggested by Johnson, my data would cuggest an annual herring consumption level of 230,000 metric tons or 44% [0.23(100)/0.53] of total stock. The range of sampling error would likely only reduce this estimate by up to 50%, still a significant consumption of herring.

It should be cautioned that reduction in dogfish numbers does not automatically imply that large increases of particular species available to commercial fisheries will result, as other predators, which are themselves preyed upon by dogfish, may also increase in numbers and check the expansion of such species.

LITERATURE CITED

Aasen, O. 1962. Norske pigghamerkinger 1958-61. Fiskets Gang, 48: 507-511.

1963. Length and growth of the porbeagle (Lamna nasus Bonnaterre) in the North West Atlantic. Fiskdir. Skr., Ser. Havinnders, 13(6): 20-37.

Allen, K.R. 1966. A method of fitting growth curves of the von Bertalanffy type to observed data. J. Fish. Res. Bd. Canada, 23: 163-179.

Alverson, D.L., and M.E. Stansby. 1963. The spiny dogfish (Squalus acanthias) in the northeastern Pacific. U.S. Fish Wldlf. Ser., Spec. Sci. Rpt. (Fish.) No. 447, 25pp.

Anonymous. 1952. Contrast in dogfish migrations. Fish. Res. Bd. Canada, Prog. Rpt. Pac. No.92: 20.

1975. British Columbia catch statistics 1974. Canada Dept. Environ., Fish. Mar. Serv. - Pac. Region, Vancouver, 215 pp.

Bailey, R.M., J.E. Fitch, E.S. Herald, E.A. Lachner, C.C. Lindsey, C.R. Robins, and W.B. Scott. 1970. A list of common and scientific names of fishes from the United States and Canada (3rd ed.). Amer. Fish. Soc., Spec. Publ. No.6, 150 pp.

Barraclough, W.E. 1948. The sunken gill-net fishery, and an analysis of the availability of the dogfish (Squalus suckleyi Girard) and the soup-fin shark (Galeorhinus galeus Linnaeus) in British Columbia waters from 1943 to 1946. M.A. Thesis, University of British Columbia, 61 pp.

Benzer, P. 1944. Morphology of calcification in Squalus acanthias. Copeia, 1944: 217-224.

Berry, J. 1965. The use of vertebral rings to determine age and growth of Raja eglanteria, the clearnose skate, in Delaware Bay. M.Sc. Thesis, University of Delaware, 53 pp.

Bigelow, H.B., and W.C. Schroeder. 1948. Fishes of the Western North Atlantic: lancelets, cyclostomes, and sharks. Mem. Sears Fnd. Mar. Res., 1, 576 pp.

1957. A study of the sharks of the suborder Squaloidea. Bull. Mus. Comp. Zool., 117(1): 1-150.

Bonham, K. 1954. Food of the dogfish, Squalus acanthias. Wash. Dept. Fish., Fish. Res. Pap., 1(2): 25-26.

Bonham, K., F.B. Sanford, W. Clegg, and G.C. Bucher. 1949. Biological and vitamin A studies of dogfish (Squalus suckleyi) landed in the State of Washington. Wash. Dept. Fish., Biol. Bull. No. 49A: 83-114.

Brett, J.R., and J.M. Blackburn (in press) Aquaculture program: dogfish bioenergetics. 1974 Annual Rpt., Fish. Res. Bd. Canada.

Calaprice, J.R., H.M. McSheffrey, and L.A. Lapi. 1971. Radioisotope X-ray fluorescence spectrometry in aquatic biology: a review. J. Fish. Res. Bd. Canada, 28: 1583-1594.

Chatwin, B.M., and C.R. Forrester. 1953. Feeding habits of dogfish (Squalus suckleyi Girard). Fish. Res. Bd. Canada, Prog. Rpt. Pac. No. 95: 35-38.

Clark, E. 1963. The maintenance of sharks in captivity with a report on their instrumental conditioning, pp.115-149. In P.W. Gilbert (ed.) Sharks and survival. Heath, Boston, 578 pp.

Clemens, W.A., and G.V. Wilby. 1961. Fishes of the Pacific coast of Canada. Bull. Fish. Res. Bd. Canada No. 68 (2nd ed.), 443 pp.

Daiber, F.C. 1960. A technique for age determination in the skate, Raja eglanteria. Copeia, 1960: 258-260.

Dao, J. 1974. An automated scanning electron microscope/electron microprobe for chemical and biological research. American Laboratory, Sept. 1974, 6 pp.

Doyle, J. 1968. Ageing changes in cartilage from Squalus acanthias L. Comp. Biochem. Physiol., 25: 201-206.

Ford, E. 1921. A contribution of our knowledge of the life-histories of the dogfishes landed at Plymouth. J. Mar. Biol. Assoc. U.K., 12: 468-505.

Forrester, C.R. 1972. Pectoral fin length in the dogfish Squalus acanthias off British Columbia. J. Fish. Res. Bd. Canada, 29: 1211-1212.

Garrick, J.A.F. 1960. The species of Squalus from New Zealand and Australia; and a general account and key to the New Zealand Squaloidea. Trans. Roy. Soc. New Zealand, 88(3): 519-557.

Hart, J.L. 1973. Pacific fishes of Canada. Bull. Fish. Res. Bd. Canada No.180, 740 pp.

Haskell, W.L. 1949. An investigation of the possibility of determining the age of sharks through annuli as shown in cross sections of vertebrae. Ann. Rept. Mar. Lab., Texas Game, Fish, and Oyster Comm., Fiscal year 1948-1949: 212-217.

Hogben, C.A.M. 1967. Secretion of acid by the dogfish *Squalus acanthias*. In P.W. Gilbert, R.F. Mathewson, and D.P. Rall (eds.) Sharks, skates, and rays. Johns Hopkins, Baltimore, 624 pp.

Holden, M.J. 1966. The food of the spurdog, *Squalus acanthias* (L.). J. Cons. Perm. Int. Expl. Mer, 30: 255-266.

1967. Transatlantic movement of a tagged spurdogfish. Nature, 214: 1140-1141.

1973. Are long-term sustainable fisheries for elasmobranchs possible? In B.B. Parrish (ed.), Fish stocks and recruitment, Rapp. Proc.-Verb. Reun., Cons. Int. Expl. Mer, 164: 360-367.

Holden, M.J., and P.S. Meadows. 1962. The structure of the spine of the spur dogfish (*Squalus acanthias* L.) and its use for age determination. J. Mar. Biol. Assoc. U.K., 42: 179-197.

Holland, G.A. 1957. Migration and growth of the dogfish shark, *Squalus acanthias* (Linnaeus), of the eastern North Pacific. Wash. Dept. Fish., Fish. Res. Pap., 2(1): 43-59.

Ishiyama, R. 1951. Studies on the rays and skates belonging to the family Rajidae, found in Japan and adjacent regions. 2. On the age-determination of Japanese black-skate, *Raja fusca* Garman. Bull. Jap. Soc. Sci. Fish., 16: 112-118.

Jensen, A.C. 1966. Life history of the spiny dogfish. U.S. Fish Wldlfe. Serv., Fish. Bull., 65: 527-554.

Jones, B.C. 1974. G.B. Reed groundfish cruise no. 74-2, March 4-15, 1974. Fish. Res. Bd. Canada, Man. Rpt. Ser. No. 1302, 15 pp.

Kaganovskaia, S.M. 1933. A method of determining the age and the composition of the catches of the spiny dogfish (*Squalus acanthias* L.). Bull. Far Eastern Acdmy. Sci. USSR, No. 1-3: 139-141. (Trans. from Russian for Fish. Res. Bd. Canada, No.281)

1937. Contribution to the biology of the spiny shark (*Squalus acanthias* L.). Bull. Pac. Sci. Inst. Fish. Ocean. USSR, 10: 105-115. (Trans. from Russian for Int. Fish. Comm., U. Wash., No.2198)

Kato, S., S. Springer, and M.H. Wagner. 1967. Field guide to eastern Pacific and Hawaiian sharks. U.S. Fish Wldlf. Serv., Bur. Comm. Fish. Circ. No. 271.

Ketchen, K.S. 1969. A review of the dogfish problem off the west coast of Canada. Fish. Res. Bd. Canada, Man. Rpt. Ser. No. 1048, 25pp.

1972. Size at maturity, fecundity and embryonic growth of the spiny dogfish (*Squalus acanthias*) in British Columbia waters. J. Fish. Res. Bd. Canada, 29: 1717-1723.

1975. Age and growth of dogfish (*Squalus acanthias*) in British Columbia waters. J. Fish Res. Bd. Canada, 32: 43-59.

Kohler, A.C., D.N. Fitzgerald, R.G. Halliday, J.S. Scott, and A.V. Taylor. 1969. Length-weight relationships of marine fishes of the Canadian Atlantic region. Fish. Res. Bd. Canada, Tech. Rpt. No. 164.

Lindberg, G.U., and M.I. Legeza. 1956. On two forms of spiny dogfish, *Squalus acanthias* L. Zool. Zh., 35: 1685-1688. (Prelim. trans. from Russian by S. Uzelac of Simon Fraser University; lodged at library of Pac. Biol. Stn., Nanaimo, B.C.)

1959. Fishes of the Sea of Japan and the adjacent areas of the Sea of Okhotsk and the Yellow Sea. Zool. Inst. Acad. Sci. USSR, 68, 198 pp. (Trans. from Russian by Israel Prog. Sci. Trans., Jerusalem, 1967)

Love, R.M. 1970. The chemical biology of fishes. Acad. Press, New York, 547 pp.

Lucas, V.Z. 1930. Notes on the life-history of *Squalus sucklii* Girard. Mimeo. Rpt., Pac. Biol. Stn., Nanaimo, B.C., 6pp.

Manwell, C. 1963. Fetal and adult hemoglobins of the spiny dogfish *Squalus suckleyi*. Arch. Biochem. Biophys., 101: 504-511.

Mayr, E. 1969. Principles of systematic zoology. McGraw-Hill, Toronto, 428 pp.

Pienaar, L.V., and J.A. Thomson. 1969. Allometric weight-length regression model. J. Fish Res. Bd. Canada, 26: 123-131.

Pugsley, L.I. 1940. Factors influencing the vitamin A and D potency of grayfish liver oil *Squalus sucklii* (Girard). J. Fish. Res. Bd. Canada 4: 312-322.

Rae, B.B. 1961. Dogfish. Scottish Fish. Bull. No. 14: 14-19.

Razum, A. 1952. Foods of the dogfish, *Squalus acanthias*, and the brown smoothhound, *Rhinotriocis henlei*, in San Francisco Bay, California. M.A. Thesis, University of California, 57 pp.

Rhodes, J.R. 1966. Radioisotope X-ray spectrometry: a review. The Analyst, 91(1088): 683-699.

Shepard, M.P., and J.C. Stevenson. 1956. Abundance, distribution and commercial exploitation of the fisheries resources of Canada's west coast. Trans. 9th B.C. Nat. Res. Conf., February, 1956: 131-191.

Simkiss, K. 1974. Calcium metabolism of fish in relation to ageing, pp.1-12. In T.B. Bagenal (ed.), Ageing of fish, Proceedings of an international symposium at the University of Reading, England, July 19-20, 1973, Unwin Bros., Surrey, England, 234 pp.

Simpson, T.H., and C.S. Wardle. 1967. A seasonal cycle in the testis of the spurdog, *Squalus acanthias*, and the sites of 3B-hydroxysteroid dehydrogenase activity. J. Mar. Biol. Assoc. U.K., 47: 699-708.

Springer, S. 1967. Social organization of shark populations, pp.149-174. In P.W. Gilbert, R.F. Mathewson, and D.P. Rall (eds.), Sharks, skates, and rays. Johns Hopkins, Baltimore, 624 pp.

Springer, V.G., and J.A.F. Garrick. 1964. A survey of vertebral numbers in sharks. Proc. U.S. Nat. Mus., 116: 73-96.

Stevens, J.D. 1975. Vertebral rings as a means of age determination in the blue shark (*Prionace glauca* L.). J. Mar. Biol. Assoc. U.K., 55: 657-665.

Templeman, W. 1944. The life-history of the spiny dogfish (*Squalus acanthias*) and the vitamin A values of dogfish liver oil. Nfdld. Dept. Nat. Res., Res. Bull. (Fish.) No.15, 102pp.

1958. Grand Bank tagged dogfish moves to Iceland. Fish. Res. Bd. Canada, Prog. Rpt. Atl. No.70: 28-30.

Tsuyuki, H., E. Roberts, and W.E. Vanstone. 1965. Comparative zone electropherograms of muscle myogens and blood hemoglobins of marine and freshwater vertebrates and their application to biochemical systematics. J. Fish. Res. Bd. Canada, 22: 203-213.

Turner, C.E. 1965. X-ray techniques to facilitate meristic studies of Pacific salmon. Mimeo. Rpt., Pac. Biol. Stn., Nanaimo, B.C., 7 pp.

Windell, J.T. 1967. Rates of digestion in fishes, pp. 151-173. In S.D. Gerking (ed.), The biological basis of freshwater fish production. Symp. Inter. Biol. Prog., Univ. Reading, England, Sept. 1-6, 1960, Blackwell Sci. Publ., Oxford, England, 495 pp.

1968. Food analysis and rate of digestion, pp. 197-203. In W.E. Ricker (ed.), Methods of assessment of fish production in fresh waters. Inter. Biol. Prog. Hdbk. No. 3, Blackwell Sci. Publ., Oxford, England, 313 pp.

Woldseth, R. 1973. X-ray energy spectrometry. Kevex Corp., Burlingame, California.

Wolf, P.L. 1963. A comparative study on the fate of the internal yolk sac in elasmobranchs. M.Sc. Thesis, University of Delaware, 48 pp.

CURRICULUM VITAE

Name: BARRY CYRIL JONES

Place and year of birth: London, England 1939

Education: University of British Columbia, Vancouver
Faculty of Forestry, 1959-1962
Faculty of Science, 1963-1964
B.Sc. (Zoology) 1965
Faculty of Graduate Studies, 1969-1971
M.Sc. (Zoology) 1972

Simon Fraser University, Burnaby
Faculty of Science, 1972-1976
Ph.D. (Biological Sciences)

Experience: Teaching Assistant
Department of Zoology
University of British Columbia

Teaching Assistant
Department of Biological Sciences
Simon Fraser University, Spring 1973
Spring 1975
Spring 1976

Awards: B.C. Salmon Derby Research Scholarship, 1973
Simon Fraser University President's Research Grant, Summer, 1975.

Papers Published:

Jones, B.C. 1972.
Effect of intertidal exposure on survival and embryonic development of Pacific herring spawn. J. Fish. Res. Bd. Canada, 29: 1119-1124.

Jones, B.C. 1974.
G.B. Reed groundfish cruise No. 74-2, March 4-15, 1974. Fish. Res. Bd. Canada, Man. Rpt. Ser. No. 1302, 15 pp.

Jones, B.C., and G.H. Geen. 1974.
Small shark restraining apparatus. Prog. Fish-Cult., 36:115.

Jones, B.C., and G.H. Geen (in press).
Age and growth of spiny dogfish (Squalus acanthias Linnaeus) in the Strait of Georgia, British Columbia. J. Fish. Res. Bd. Canada.

A taxonomic re-evaluation of the spiny dogfish (Squalus acanthias Linnaeus) in the northeastern Pacific Ocean. J. Fish. Res. Bd. Canada.

Paper presented:
Effect of intertidal exposure on Pacific herring spawn and consequent management implications. Pacific Fishery Biologists 35th Annual Meeting, Harrison Hot Springs, B.C. March 21-23, 1973.