Investigations on the biology of Indian Mackerel *Rastrelliger kanagurta* (Cuvier) along the Central Kerala coast with special reference to maturation, feeding and lipid dynamics

Thesis submitted to

Cochin University of Science and Technology

in partial fulfillment of the requirement for the degree of

DOCTOR OF PHILOSOPHY

FACULTY OF MARINE SCIENCES

GANGA .U.

Reg. No. 2763

DEPARTMENT OF MARINE BIOLOGY, MICROBIOLOGY AND BIOCHEMISTRY
SCHOOL OF MARINE SCIENCES
COCHIN UNIVERSITY OF SCIENCE AND TECHNOLOGY
KOCHI – 682 016, INDIA

September 2010

DECLARATION

I, Ganga. U., do hereby declare that the thesis entitled **"Investigations on the biology of Indian Mackerel *Rastrelliger kanagurta* (Cuvier) along the Central Kerala coast with special reference to maturation, feeding and lipid dynamics** " is a genuine record of research work carried out by me under the guidance of **Prof. (Dr.) C.K. Radhakrishnan,** Emeritus Professor, Cochin University of Science and Technology, and no part of the work has previously formed the basis for the award of any Degree, Associateship and Fellowship or any other similar title or recognition of any University or Institution.

Ganga.U

Kochi – 16

September-2010

CERTIFICATE

This is to certify that the thesis entitled "Investigations on the biology of Indian Mackerel *Rastrelliger kanagurta* (Cuvier) along the Central Kerala coast with special reference to maturation, feeding and lipid dynamics" to be submitted by Smt. Ganga. U., is an authentic record of research work carried out by her under my guidance and supervision in partial fulfilment of the requirement for the degree of Doctor of Philosophy of Cochin University of Science and Technology, under the faculty of Marine Sciences.

Prof. (Dr.) C.K. Radhakrishnan

(Supervising Guide)

Prof. (Dr.) C.K. Radhakrishnan

Emeritus Professor

Dept. of Marine Biology, Microbiology & Biochemistry

Cochin University of Science and Technology

Kochi – 682 016

ACKNOWLEDGEMENT

I wish to place on record my sincere and heartfelt thanks to my supervising guide Dr. C. K. Radhakrishnan, for his invaluable guidance and encouragements which culminated in this thesis. I am deeply indebted to Dr. N. G. K. Pillai, Principal Scientist and Head (Retd.), Pelagic Fisheries Division, CMFRI, Kochi who encouraged me in all my endeavours, and was a well-wisher, guiding light and mentor throughout. I am greatly obliged to Prof. (Dr.) Babu Philip who served as the Subject Expert in my Doctoral Committee, for supporting me with kind advice and valuable suggestions during my research work. I thank The Director, School of Marine Sciences, CUSAT , The Dean, Faculty of Marine Sciences and The Head, Department of Marine Biology, Microbiology and Biochemistry for all facilities and support provided during the tenure of the research programme. I also place on record my gratitude to all the faculty of the Department of Marine biology, Microbiology and Biochemistry, namely, Dr. A.V. Saramma, Dr. Rosamma Philip, Dr. Aneykutty Joseph, Dr. Mohammed Hatha and Dr. Bijoy Nandan for all their valuable advice and encouragement.

I thank Prof. (Dr.) Mohan Joseph Modayil, former Director of CMFRI, for granting me study leave to carry out the work. I have immensely benefitted from the various interactions with respected senior colleagues and I place on record my sincere thanks to Dr. T. M. Yohannan, Retd. Principal Scientist, Pelagic Fisheries Division, CMFRI; Dr.E.Vivekanandan, Former Head, Demersal Fisheries Division, CMFRI ; Dr. K.S. Mohamed, Head, Molluscan Fisheries Division, CMFRI for patiently clearing several doubts and giving me valuable guidance and helpful suggestions. I am deeply indebted to Dr. T.V. Sankar, Senior Scientist, Department of Biochemistry, Central Institute of Fisheries Technology, Kochi for his invaluable guidance and help given to me while carrying out works related to biochemical analyses. Heartfelt thanks are also due to Dr. R. Anandan, Dr. P. Ashraf, Dr. K. Ashok Kumar and Dr. J. Bindu, Senior Scientists of the Central Institute of Fisheries Technology, Kochi and Dr. Pramod, MPEDA, for all their kind helps and co-operation during my research work. I also thank Dr. P. Vijayagopal of the Marine Biotechnology Division, CMFRI for giving critical suggestions and advice. I acknowledge with thanks the invaluable help given by Dr. Sobhana K.S. and Shri. K.K. Surendran while carrying out the histological studies. Mr. D.Edwin, Librarian,

CMFRI is especially thanked for enabling me to collect several valuable references from global libraries. Drs. Somy Kuriakose and J. Jayasankar are thanked for help provided for the statistical works. Help and advice provided by Dr. P.P. Manojkumar and Dr. K. K. Phillipose, CMFRI are remembered with thanks.

I specially thank Dr. G. Syda Rao, Director, CMFRI Kochi for providing all facilities and an enabling atmosphere to carry out my research work.

Senior colleagues of CMFRI Drs. P.P. Pillai, P.N.R.Nair, A.A. Jayaprakash and C.P.Gopinathan (Retd.) are gratefully remembered for their advices. I also thank Dr. E. M. Abdussamad, Mr. D. Prakasan, Shri. M.N.K. Elayathu, Smt. Rema, K.V., Shri. S. Nandakumar Rao and Shri. P. R. Abhilash, CMFRI, for their kind co-operation and helps on various occassions. Shri. K. Ganesan and Shri. K. Janardhanan are thanked for assisting me in collecting some of the fish samples during my work.

My special thanks to Shri. P.V. Devassy and Smt. P.S. Sumathi, administration Section, CMFRI as well as all the administrative staff of the Department of Marine biology, Microbiology and Biochemistry and the Library section for their kind co-operation and help always.

Special thanks are due to Hashim Manjebrayakath, SRF, Pelagic Fisheries Division, for taking an extra step and going that extra mile to help always. Shri. Akhilesh, K.V., Rajool Shanis, Bineesh. K.K., Mrs. Beni. N., and Manju Sebastine, the young and energetic SRFs of the Pelagic Fisheries Division are thanked for cheerfully chipping in with their helps whenever and wherever requested. Sincere thanks to all my friends, especially, Smt. Jenni B, Dr. Radhika, Cilla Abraham, Dr. Priyalekshmi, Dr. Anjana Mohan, Smt. N.R. Lethadevi and Smt. Bindu Sanjeev for their affection and concerned help rendered on several occassions.

I profusely thank my family, especially my parents Mrs. Geetha and Mr. T. Upendra Prabhu and my parents-in -law, Mrs. Sumangali and Mr. H. Janardhan Bhat for all their blessful kindness, understanding and encouragement throughout. Last but not least, I owe special thanks to my husband Dr. J. Jagannath Bhat and my daughters Srijitha and Anusree for all their affection, kind concerns and patience throughout.

Ganga .U

INDEX

LIST OF PLATES & FIGURES

LIST OF TABLES

LIST OF ABBREVIATIONS

AA	Arachidonic acid
DHA	Docosahexaenoic acid
DOC	Dissolved organic carbon
EPA	Eicosa pentaenoic acid
FA	Fatty acids
FOM	Final Oocyte Maturation
FOM	Final Oocyte maturation
GSI	Gonado-somatic Index
I_P	Index of Preponderance
MUFA	Mono unsaturated fatty acids
PG	Prostaglandins
PUFA	Poly un saturated fatty acids
R_S	Rank Correlation Coefficient
SFA	Saturated fatty acids

CHAPTER 1
GENERAL INTRODUCTION

CHAPTER 1

GENERAL INTRODUCTION

The Indian mackerel *Rastrelliger kanagurta* (Cuvier, 1817) is a pelagic fish that is widely distributed in the Indo-Pacific region. Along the Indian coast its fishery is only second in importance to the oil sardine *Sardinella longiceps*. During the present decade (2000- 2008) the average all India landings was estimated at 1.29 lakh tones (t) most of which was landed along the southwest coast of India especially in Kerala and Karnataka. However, recent reports indicate that climate change induced variations in the marine environment such as sea surface temperature (SST) have impacted the mackerel and sardine stocks leading to the northward extension of their distribution ranges resulting in development of new fisheries targeting mackerel especially along the northwest coast of India (Asokan *et al*., 2009).

A species can comprise of a single stock or a number of stocks with a fixed spawning ground and specific spawning season and probably a consistent migratory circuit (Begg and Waldman, 1999). From the point of fisheries management, it is observed that there is localized variation in fishing intensity along the Indian coast and therefore the stocks have to be effectively delineated and managed. To facilitate formulation of such appropriate exploitation and management strategies on local/ regional scales a holistic knowledge-base on biology, life history and behaviour of major commercial fish species in the region is crucial (Adams, 1980; Begg *et al.*, 1999). With regard to *R. kanagurta*, studies on morphometrics, food and feeding habits, maturity and spawning have

concentrated only in certain fishery centres such as off Calicut (Malabar Upwelling zone) of the state of Kerala and the Mangalore / Karwar coast of the state of Karnataka (Noble and Geetha, 1992). Relatively few reports on the fishery and biology of mackerel in other regions of its occurrence along the west coast (Rao, 1967; Kutty, 1965; Noble, 1974; Gopakumar *et al*., 1991); east coast (Rao, 1962; Abdussamad *et al*., 2006) of India as well as from the Andaman seas (Jones and Silas, 1962; Luther,1973) are available. The present study focuses on the mackerel resource available off Cochin along the Central Kerala coast where the status of the resource is not yet reported.

Plate 1. Indian mackerel *Rastrelliger kanagurta* (Cuvier, 1817)

1.1. Taxonomic classification:

ORDER: PERCIFORMES

FAMILY: SCOMBRIDAE

SUB-FAMILY : SCOMBRINAE

GENUS: *RASTRELLIGER*

SPECIES: *KANAGURTA*

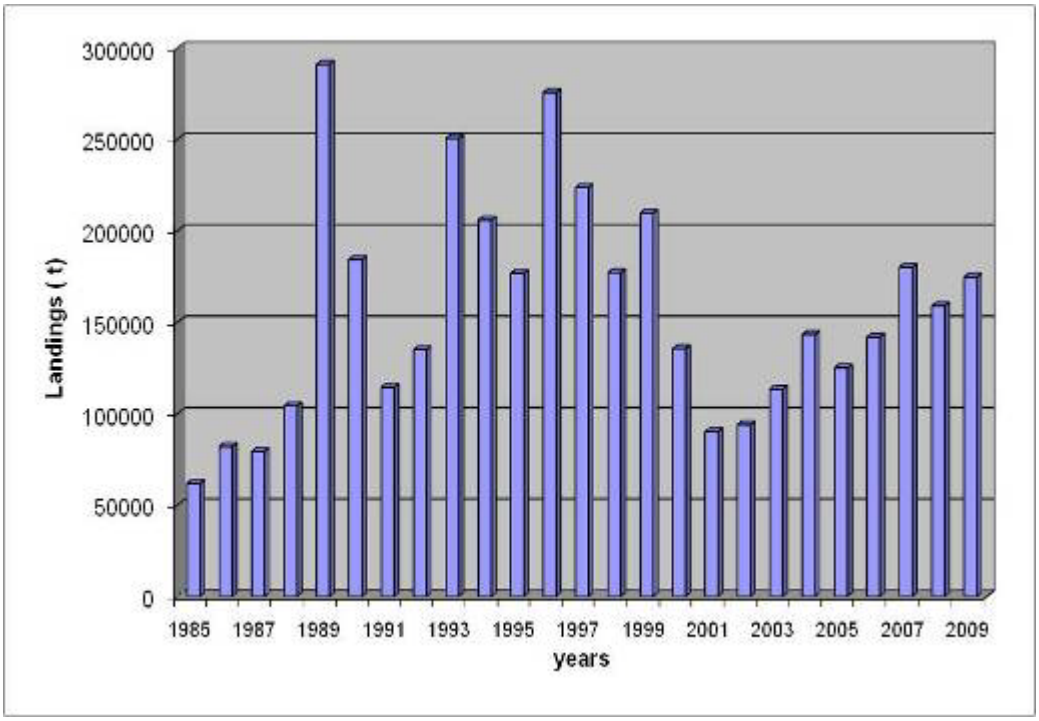
Distinguishing characters: Body bluish green with dark stripes or rows of dusky spots along upper half of the body, 2 dorsal fins, the first being spiny and the second one rayed, 5-6 pairs of anal finlets, pelvic fin without spine, snout pointed and length of head distinctly greater than depth of body (used to distinguish from another species, *R. brachysoma*).

1.2. Distribution & Fishery: *R. kanagurta* is widely distributed in the tropical Indo-west Pacific region, along both east and west coast of India and the Andaman and Nicobar Islands. Dense shoals occur in the coastal waters upto 50 m depths forming a major fishery along the west coast of India. Along the east coast, distribution and maximum abundance recorded at about 70 - 100 m depths.

The mackerel fishery along the Indian coast is essentially comprised of a single species, *R. kanagurta* although two other species namely, *R.brachysoma* (Bleeker, 1851) in Andaman seas (Jones and Silas, 1962) and *R. faughni* (Matsui, 1967) along the east coast of India (Gnanamuttu, 1971) are also recorded to occur in stray numbers. The fishery of Indian mackerel *R. kanagurta* is typically characterized by wide annual fluctuations and during the last 2 decades has varied from 113,000 t (1991) to a record high of 290,000 t in 1989 while the average all India catch during 2007- 08 was 165,000t (Fig. 1.1). Maximum exploitation of the resource has been recorded from the southwest (Kerala, Karnataka and Goa) coast of India using seines, gillnets and trawls. During the 90s a quantum leap in the annual marine fish catch was reported along the Kerala coast resulting mainly from increased catches of small pelagics

such as sardines and mackerel, which could be attributed to the introduction of an innovative gear the ring seine and motorization of country crafts as well as development of fishing harbours.

Of late the technological innovations, have led to changing fishing patterns and exploitation is spreading on temporal as well as spatial scales. Prior to 80s the monsoon season coinciding with spawning and recruitment of marine fishes along the southwest coast was an unofficial closed season due to the rough weather. But technological innovations in the fishing crafts and gears as well as the development of fishing harbours paved the way for exploitation even during monsoon by the early 90s. By the late 90s a sizeable portion of the mackerel caught by ring seines along the Malabar coast occurred during the monsoon period coinciding with their peak breeding and juveniles or first time spawners formed major portion of the catches which led to suggestions for exercising caution in such large scale capture (Yohannan and Nair, 2002). During 2005-08 period, the average annual mackerel catch along the Kerala coast was 55,380 t which was landed mainly by ring seines, followed by outboard gill nets and trawls. Nearly 11% of this catch was from the Central Kerala belt comprising the coastal districts of Ernakulam and Alappuzha. Although the fishery occurred throughout the year, peak catches were recorded during the monsoon (June – September) period followed by the post monsoon period (October – January).



Source: CMFRI Annual Reports

Fig. 1.1. All India landings (t) of Indian mackerel during 1985 -2009

1.3. Length composition: Yohannan and Sivadas (2003) reported that the average length frequency distribution of mackerel along the west coast of India is constituted by size group 110 – 150 mm with mode at 145 mm, while along the east coast, larger size groups of 175 -215 mm with modal size 195 mm are recorded. During the period 2004 -2008, the mackerel landings off Cochin were mainly constituted by the 190 - 200 mm size group (64% in numbers landed) with the average season-wise length frequency as given in Fig. 1.2. Earlier, Noble (1974) had reported that mainly juveniles < 190 mm dominated in the fishery along the Cochin coast which was carried out using gill nets in inshore waters. The subsequent introduction of ring seines by larger motorized/mechanized

crafts which extended the area fished to deeper waters than that exploited during the 80s may explain the landings of larger size groups subsequently.

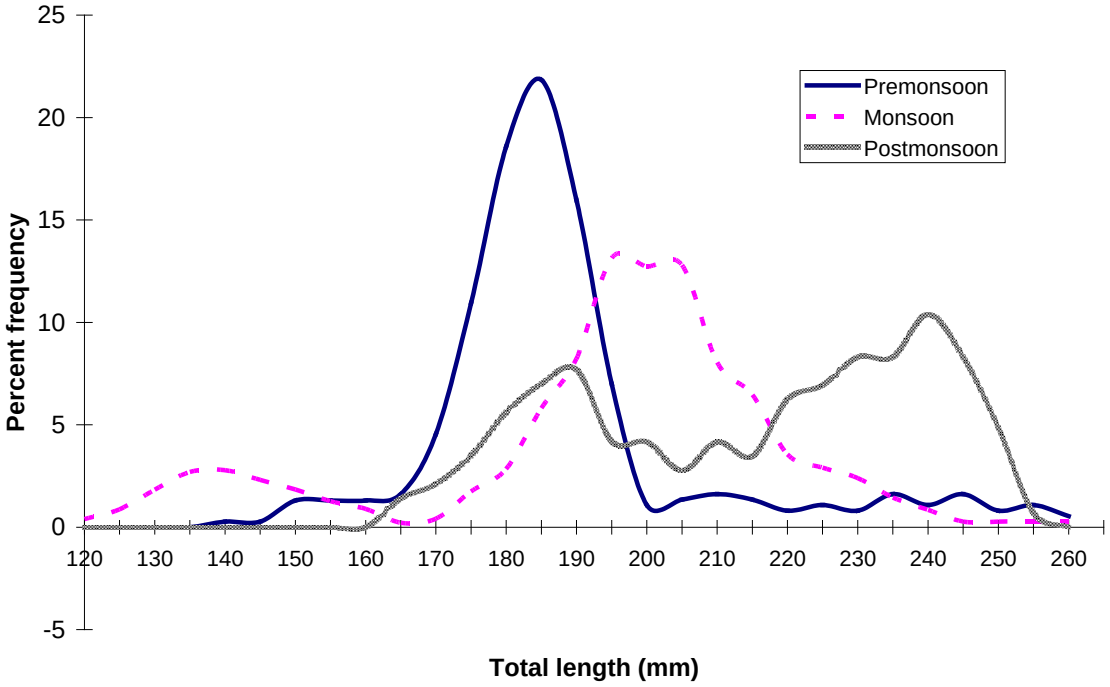


Fig.1.2. Seasonal length frequency distribution of mackerel caught by ring seines and trawls along the Central Kerala coast (2004 - 2008 average)

1.4. Age and growth: The life span of mackerel is believed to be about two years and growth is very fast especially in the juvenile stages, with fishes reaching a length of about 190 mm by the end of first year (Devaraj *et al*., 1997).

1.5. Maturation and spawning biology: Peak spawning and recruitment is reported to be coinciding with the southwest and northeast monsoon seasons on the west and east coasts of India respectively (Qasim, 1973). The FAO/UNDP assisted exploratory surveys of pelagic resources considers the central Kerala

belt as an important spawning area of the Indian mackerel (Anon., 1976). However detailed studies on the maturity and spawning dynamics of mackerel in other regions including off Cochin coast are few.

Plate 2. Different size groups of *R. kanagurta* occurring in the mackerel landings

1.6. Food and feeding habits: The Indian mackerel has been variously classified as a planktonivore/ omnivore with varied diet composition (diatoms, dinoflagellates, copepods, crustaceans and occasionally fish and sand particles) recorded by researchers in various fishery centres along the Indian coast

(Vivekanandan *et al*., 2009). Except a few reports based on stray landings of mackerel from deep sea trawlers conducting exploratory surveys from the northwest coast observations on diet composition of mackerel are mostly from inshore waters of < 20 m depths (Kutty, 1965; Rao, 1965). It has been hypothesized that the microbial loop in the coastal waters may be a significant factor ensuring adequate energy to allow reproduction and recruitment successfully in mackerel even when the environmental conditions and food availability are generally unfavourable to support successful recruitment process of another pelagic species, the oil sardine, sharing the same ecosystem with mackerel (Madhupratap *et al*., 1994). Detailed studies on the seasonal and ontogenetic changes in the diet composition, qualitative aspects of the diets and feeding dynamics in relation to the spawning/maturation cycle are not reported for the Indian mackerel.

1.7. Behaviour and Stock studies: Studies on the fishery by commercial vessels as well as the FAO-UNDP conducted acoustic and exploratory fishing surveys have indicated that the species remains in the shelf waters year around (Anon., 1976). Mackerels have a tendency to remain in the mixed layer, just above the thermocline where food availability is good. With the beginning of the sinking of thermocline starting sometime by November in the Arabian Sea they also move to deeper waters which results in declining catches from surface gears such as seines and appearance in the bottom-set gears such as trawls (Yohannan and Abdurahiman, 1998). Large scale occurrence / migration of juvenile mackerel in inshore region during the period immediately following the

monsoon has been recorded. Morphometric/meristic studies, tagging, electrophoretic as well as DNA techniques have been applied in *R. kanagurta* stock studies (Seshappa, 1985; Menzes *et al*., 1993; Jayasankar and Dharmalingam, 1997). According to Nair *et al*. (1970) the few tagging studies conducted suggest limited offshore migration and probably a long-distance north-south migration along the west coast of India. However, he concluded that a number of independent and discrete populations of *R. kanagurta* exist within a single stock in Indian waters. Later, genetic studies using DNA markers (Jayasankar and Dharmalingam, 1997) suggested restricted intermixing of populations which supports the observations of Nair *et al*. (1970). The stock is believed to be optimally exploited along the Indian coast and showing regional variations in fishing mortality rates (Noble *et al*., 1992; Devaraj *et al*., 1994; Yohannan *et al*., 2002). The less exploited deeper waters are believed to serve as natural refuges of the resource making it strong enough to withstand high fishing mortalities especially along the west coast of India (Yohannan *et al*., 2002).

2. Background of the study: An understanding of the reproductive biology of a species is an important prerequisite for providing scientific advice for fisheries management to enable optimum exploitation of the concerned species in tune with its reproductive characteristics. Some of the important life-history traits of fishes which determines the productivity of the resource which can be usefully integrated into scientific advice for fisheries management include the size/age at first maturity, sex ratio, fecundity, spawning periods and spawning behaviour

(Katsukawa, 1997; Morgan, 2008). There is a longstanding interest in fish lipids due to the fact that they play an important role in the life-histories and physiology of fish as well as the fact that they contain highly unsaturated fatty acids that are particularly important in the nutrition of many animals including humans. The major role of lipids in fish is for the storage and provision of metabolic energy in the form of ATP provided through ß oxidation of fatty acids (Sargent *et al*., 2002). Lipid energy has therefore been considered as a proxy for egg production and reproduction in several fish stocks for assessment of recruitment and stock abundance that is likely to follow (Marshall *et al*., 1999; Kamler, 2005). It is also sufficiently well documented that all fish species have a unique and specific fatty acid composition and the critical factor determining the species level fatty acid composition is the specificity of enzyme regulated fatty acid oxidation of the various fish species (Tocher, 2003). The specific fatty acid composition is reportedly important not only for the well being of the particular fish species, especially in ensuring successful reproduction, larval survival and growth to adult stage but also in terms of providing health promoting fatty acids such as Docosahexaenoic acid (DHA) and Eicosapentaenoic acid (EPA) to human consumers. Maturation and recruitment dynamics of marine fish is critically dependant on availability of food resources (Wootton,1985) and diet is considered a critical factor regulating reproductive success in fishes especially through their control on polyunsaturated fatty acid (PUFA) content (Sargent *et al*., 1999). According to Kraak *et al*. (1998), PUFAs being important regulators of steroid biosynthesis in fishes are influenced by their diet and represent an

important signal underlying the dietary modulation of reproductive functions in fish. Thus, in wild fish stocks who obtain their energy sources from natural feeds, environment induced adverse feeding conditions can constrain reproduction process which will in turn negatively impact their recruitment to the fishery (Lauth and Olson, 1996). This means that studies on the commercial fishery resources should also be related to the food energy available to sustain the resource. For this, information on feeding strategies for utilization of available food resources and feeding preferences of the different size/ maturity groups of many commercially important fish species in Indian seas is required but available literature is rather scanty. The present study therefore was aimed at understanding the dynamics of the *R. kanagurta* resource using a holistic approach integrating information on the maturation, feeding and lipid dynamics from a relatively less studied region, namely, the Central Kerala coast on the west coast of India.

3. Study Area: The state of Kerala has a coastline of about 560 Km and the central zone comprises the coastal districts of Ernakulam and Alleppey. This region has an extensive system of backwaters and also falls within the upwelling ecosystem of the south-west coast of India. The region has rich diversity and supports substantial marine and estuarine fisheries (Menon *et al*., 2000). The mackerel fishery which is generally

Fig. 1.3. Map Showing location of study area

poor in the southern zone comprising districts of Trivandrum and Quilon shows increase in the central zone and progressive increase in catches is recorded from further northern districts of Kerala such as off Calicut (Kozhikode district) which is the Malabar upwelling ecosystem.

****

CHAPTER 2
MATURATION DYNAMICS

CHAPTER 2

MATURATION DYNAMICS

2.1. Introduction

Fishery management requires knowledge of different aspects of the reproductive biology of the fishes. This is because of the fact that the productivity of the resource is to a very large extent influenced by the reproductive traits of the particular species which in turn determine its resilience capacity and to what level the resource can be sustainably exploited by the fisheries sector (King, 1995). Each fish species has a unique set of reproductive characters (pattern of gamete development, duration of spawning season and associated endocrine changes) which can be used in formulating capture fisheries management policies (Macer, 1974; Johannes, 1978; Kathirvelu *et al.*, 2003) as well as in controlled fish breeding programmes for mariculture (Poortenar *et al.*, 2001).

Marine fishes exhibit wide heterogeneity in reproductive strategies and tactics with the main objective being to maximize progeny in relation to available energy and parental life expectancy that will reach adulthood to further propagate the species (Balon, 1984; Lambert and Ware, 1984; Ware, 1984; Wootton, 1985). The reproductive strategy of a species is the overall pattern of reproduction common to the individuals of a species whereas the reproductive tactics are those variations in response fluctuations in the environment (Wootton, 1985). A key issue in the estimation of the egg production and resilience potential in any fish species is to correctly identify its reproductive strategy that includes oocyte development pattern, fecundity type and spawning pattern (Holden and

Raitt, 1974; Smith and Walker, 2004; Murua and Saborido-Rey, 2003). It is also necessary to estimate fecundity and establish fecundity – size (length/weight/age) relationships to scale estimates of spawning stock biomass or spawner abundance to the population egg abundance which can aid a prediction of the following recruitment to the fishery (Rickman *et al*., 2000; Murua *et al.*, 2003).

As the reproductive potential of individual fishes within the spawning stock affects recruitment most fish biomass assessment programmes require inputs on reproductive parameters such as the age/length at maturity, proportion of mature fishes in the population, fecundity and spawning frequency (Nikolskii, 1969; Connover, 1985; Parrish *et al.*, 1986; Rothschild, 1986; Lambert, 1990; Koslow, 1992; Kjesbu *et al.,* 1996a; Trippel *et al.,* 1997; Marshall *et al.,* 1998; Rickman *et al.*, 2000; Rose *et al.*, 2001; Scott *et al.*, 2005). Thus, results from studies on fish maturation dynamics using exploratory surveys for estimation of spawner, egg and larval biomass, application of macroscopic staging of gonads and histological interpretation of ovarian development pattern and estimates of reproductive parameters have been widely applied to formulate capture fisheries management strategies such as enforcement of minimum catch at size restrictions, closed fishing seasons during peak breeding periods as well as in aquaculture sector for improved breeding technologies (Poortenar *et al.*, 2001; Murua and Saborido-Rey, 2003; Smith and Walker, 2004).

Taking into consideration the above, the present study focuses on the Indian mackerel which is an important pelagic resource contributing nearly 6% of

the total marine fish landings of India. The resource is a major component of the landings along the southwest coast of India especially Kerala and Karnataka with wide fluctuations in annual landings. Although its fishery biology with regards to maturation, spawning and recruitment is relatively well studied from the Malabar upwelling ecosystem of Kerala, relatively little information is available from the Central Kerala belt which is a different and unique ecosystem (Menon *et al*., 2000). This region has been identified as the major spawning gyre of the Indian mackerel based on fish and larval surveys (Anon., 1976) but there are hardly any literature regarding its maturation and spawning dynamics from this area.

2.2. Review of literature

2.2.1. Maturation and Spawning: Spawning patterns and precise maturity ogives are critical inputs in fish stock assessments. Growth, maturation, fecundity and timing of spawning are interrelated and vary both within and among fish stocks and have been used to identify natural stock units as well as estimate spawning stock sizes in wild fish populations (Begg *et al*., 1999). According to Beverton (1992) appreciation of the demographic significance of maturation in marine fish in relation to size and age was realized by year 1900 but was applied in fishery science much later. In most of the tropical marine fishes, maturation is a continuous process resulting in the occurrence of mature fishes throughout the year (Longhurst and Pauly, 1987). However climato-hydrographical factors such as rainfall, water temperature and wind act independently or in combination as a kind of stimulus for gonad development to create peak spawning in certain

months of the years (Weber, 1974; Sundararaj, 1981; Lam, 1983; Peter and Yu, 1997; Nath *et al.*, 2007).

Maternal attributes and condition can affect fish maturity and reproductive performance (McEvoy and McEvoy, 1992; Scott *et al*., 1999; Marteinsdottir and Begg, 2002; Blanchard *et al.*, 2003; Morgan and Lilly, 2006). More recently attention is being given to male reproductive characteristics also in relation to offspring production (Trippel, 2003; Kamler, 2005). Rajasilta (1992) reported that maturation rate is dependant on fish condition with well-feeding fish maturing at a higher rate, with larger gonads and reproducing earlier than those which feed less well. Ware and Tanasichuk (1989) reported maturation rate of Pacific herring to be size dependant with larger fish maturing first. Similar observations of size related maturation have been recorded in certain pelagic fishes such as atherinids (Moreno *et al.*, 2005).

Several studies have also indicated long term changes in growth patterns and age/length at maturity for several fish stocks (Jorgensen, 1990 - Atlantic cod *Gadus morhua*; Rjindsorp, 1993- North sea Plaice *Pleuronectes platessa*; Agnalt, 2006 – mackerel *Scomber scombrus*; Silva *et al.*, 2006 - Sardines *Sardinella* spp.). Some of these changes in maturation patterns are possibly fishery-induced and have been interpreted as compensatory density – dependant effects that regulate population growth (Bowering, 1989; Jorgensen, 1990; Rjindsorp, 1993, Helser and Almeida, 1997; Rose *et al.*, 2001; Olsen *et al.*, 2004; Ernande, 2008). However, contrary to these observations, Junquera *et al.* (2004) has noted stability in the reproductive parameters in the halibut fish in spite of the temporal

changes in stock sizes over a period of 9 years. Density dependant changes in maturation can arise from food limitation due to increased intra-specific competition that directly limits energy supply for gonad development (Morgan, 2004) or indirectly impacts growth which influences the trigerring of maturation (Engelhard and Heino, 2004). An earlier age at maturity and an increase in the length specific fecundity is considered a mechanism to ensure high reproductive output when the spawning stock decreases (Koslow, 1995; Trippel *et al.*, 1997).

Hilborn and Walters (1992) suggested that spatial variations in maturation within the boundaries of a stock should also be taken into account in stock assessment if they are associated with large spatial differences in population abundance. Agnalt (2006) studying the long-term changes in growth and age at maturity of mackerel *Scomber scombrus* from North sea, related the decline in size/age at maturity during the 80s to immigration of another stock. Wang *et al.* (2009) showed how sampling biases can affect estimates of length/ age at 50% maturity and suggested need to monitor maturation schedules via multiple maturation indices.

From Indian seas, studies on maturation and spawning of several commercial species are available (Prabhu, 1955- Ribbonfishes; Prabhu, 1956; Pradhan, 1962- flatfish *Psettodes erumei*; Raju 1964, 1964a - skipjack tuna *Katsuwonus pelamis*; Dharmamba, 1959; Annigeri, 1963; Antony Raja, 1964, 1971; Radhakrishnan, 1967; Dhulkhed, 1968 - sardines and clupeids ; Sekharan, 1958; Radhakrishnan, 1965; Rao, 1967 - Indian mackerel; Appa Rao, 1964; Devadoss, 1969 - sciaenids; Marichamy, 1970 - anchovies; Kagwade, 1968 -

carangid *Caranx kalla*; Kagwade, 1970- Threadfins *Polynemus* spp.; Krishnamoorthi, 1971-Threadfin bream *Nemipterus japonicus*; Marichamy,1971- Spotted herring *Herklotsichthys punctatus*; Rangarajan, 1971- Snapper *Lutianus kasmira*; Selvaraj and Rajagopalan, 1973, Rao and Krishnan, 2009 - Rock cod *Epinepheleus* spp.; James and Vasudevappa, 1978 – catfish *Tachysurus dussumieri*; Pati, 1982- silver pomfret *Pampus argenteus*; Devaraj, 1983 - Seerfishes *Scomberomorus* spp.; Rao, 1983 - Lizard fishes *Saurida* spp.; James and Badrudeen, 1986 - Leiognathids; Rajaguru, 1992- Flatfishes; Zacharia and Jayabalan, 2007 – whitefish *Lactarius lactarius*). In the Indian seas the main spawning season of many marine fishes including *R. kanagurta* is reported to coincide with the southwest and north-east monsoons along the west and east coasts respectively (Qasim, 1973; Weber, 1974). Yohannan and Nair (2002) reported that the main spawning season of *R.kanagurta* along the southwest coast occurs during May to July and the successful broods produced during this time are the ones that support the fishery of the ensuing season. Off the Cochin coast, Noble (1974) noted a general dominance of juveniles only and very few mature mackerel in the commercial landings by gill nets. According to Antony Raja (1971) in oil sardine unfavorable ecological conditions inhibit the normal maturation process thereby constraining the recruitment process. Maturation schedules have been reported to shift in *Nemipterus* spp. with the species showing a maximum spawning season trend towards cooler climatic conditions (Vivekanandan, 2009). Such climate-change induced impacts if any, probably

due to sea water temperature rise have not yet been studied for other species including mackerel in the Indian seas.

2.2.2. Length at first maturity (L_m): This is the mean length at which fish of a given population develop ripe gonads for the first time (Froese and Pauly, 2010). The length at first maturity (L_m) is an important parameter influencing fecundity of fish and has to be assessed as shifts in the age or size at maturation have been documented for a number of exploited populations (Rothschild, 1986). Studies conducted during the 40s to 60s period have indicated the length at first maturity (L_m) of mackerel to be at 190- 224 mm length (Devanesan and John, 1940; Pradhan and Palekar, 1956; Rao, 1967). Sekharan (1958) reported that at the time of first spawning, mackerel are about two years old and measuring 200 - 220 mm in total length. In comparison, studies on Indian mackerel sampled from Andaman seas were reported to have high L_m of 250 – 259 mm (Luther, 1973) which was attributed to the presence of only large size groups available for the study. However, some recent studies indicate a significant decline with an L_m of 170 -180 mm (Prathibha and Gupta, 2004; Sivadas *et al.*, 2006).

2.2.3. Gametogenesis: Fish have evolved to reproduce under environmental conditions favorable to the survival of the eggs and larvae and long before spawning, seasonal cues begin the process of maturation. When the gonads have matured, a favourable environmental stimuli (changes in photoperiod, temperature, rainfall and food availability) can trigger ovulation and spawning (Lam, 1983; Stacey, 1984).The environmental conditions which play a key role in fish reproduction by affecting fecundity levels and thereby controls recruitment in

wild fish populations (Kjesbu *et al.*, 1998; Rjindsorp, 1991; Koslow *et al.*, 1995) are reported to be mediated by the neuroendocrine regulatory mechanisms that act via the hypothalamo-hypophyseal-gonadal axis (Nath *et al.*, 2007). During the reproductive process of female fishes, two major physiological events occur- 1) gradual enlargement of ovaries due to formation and yolky oocytes known as vitellogenesis mediated by the gonadotropin GTH1 and 2) maturation, ovulation and spawning of yolky oocytes mediated by the gonadotropin GTH2 (Nagahama, 2000). Basic patterns of oocyte growth in all species can be divided into five phases, namely, primary oocyte growth, cortical alveolar stage, vitellogenesis, maturation and ovulation (West, 1990; Tyler and Sumpter, 1996). Changes in plasma levels of gonad steroids and oocyte development in several marine teleosts (Whitehead *et al.*, 1983; Pankhurst and Conroy, 1988; Matsuyama *et al.*, 1990, 1991; Kjesbu *et al.*, 1996; Roberts, 1999; Poortenar *et al.*, 2001; Sun and Pankhurst, 2004; Sabet *et al*., 2009) has been reported. In several species including scombroids a protracted spawning period termed a bet-hedging strategy which is aimed at taking advantage of prey availability and optimizing larval survival is observed (Lambert and Ware, 1984).

Many multiple spawners have rhythmic periodicity of reproductive behavior with spawning confined to limited period of day or night (Devanesan and John, 1940; McEvoy and McEvoy, 1992). Schaefer (1998) noted diel pattern in ovarian maturation and spawning of yellow fin tuna while Shirashi *et al.* (2005) observed a lack of population synchrony in gonad development of captive chub mackerel *Scomber japonicus* after injection with human chorionic gonadotropin.

In aquaculture knowledge of timing of successive ovulations is critical as the ovulated eggs which are retained in the ovary lumen are to be removed by manual stripping of ripe females within a specified period of time, otherwise they will be over-ripened and lose their viability (McEvoy and McEvoy, 1992). Energy required to carry out the gametogenic process in fishes is usually obtained using directly ingested food (opportunistic pattern) or stored reserves from muscle/liver/other organs (conservative pattern) and is used to define the reproductive pattern in fishes (Darriba *et al.*, 2005).

2.2.4. Ovary development and classification: On the basis of oocyte size distribution, ovaries of teleosts have been classified into three basic types, synchronous, group synchronous and asynchronous (Wallace and Selman, 1981). In synchronous spawners (eg. *Salmo salar*, *Clupea harengus*) all oocytes develop and ovulate at the same time and further replenishment from earlier stages does not occur and hence due to a single spawning batch in a season show a narrow size distribution of oocytes. In group-synchronous spawners, ovaries contain two groups of oocytes, one homogenous group with larger oocyte diameter (defined as a “clutch”) and a heterogenous group of smaller oocytes from which “clutches” are formed periodically. The fishes with asynchronous development pattern have protracted spawning seasons with multiple spawnings and there is continuous recruitment of ova into maturation/ovulation, with ovaries characterized by many different sized oocytes accumulating yolk (Murua and Saborido-Rey, 2003). Asynchronous oocyte development is supposed to be adaptive to an environment where either the environmental conditions are

conducive for a prolonged breeding period or where the environmental conditions are extremely unstable in the short term so that reproductive effort can be invested profitably at the most opportune time (Lambert and Ware, 1984). In contrast, synchronous oocyte development is considered as a specialized characteristic, possibly restricted to species which make long energy-demanding migrations to spawning grounds (DeVlaming, 1983; Kjesbu *et al.*, 1998). Among asynchronous development patterns, determinate and indeterminate spawners are distinguished, based on the presence and absence respectively, of a size gap between maturing (vitellogenic oocytes) and immature (pe-vitelllogenic) eggs. In species with determinate fecundity the standing stock of vitellogenic oocytes is fixed prior to onset of spawning whereas in those species exhibiting indeterminate fecundity *de novo* vitellogenesis continues even after the onset of spawning (Murua *et al.*, 2003). From the perspective of fish life-history tactics, repeated oogenesis (indeterminate fecundity pattern) during the spawning season requires faster maturation of oocyte, but it enables a fish to adjust its reproductive investment more economically in accordance with its body condition, energy budget and availability of food (McDowall and Eldon, 1997). However in few species no consensus has been reached regarding determinate/indeterminate fecundity (Greer Walker *et al.*, 1994; Mcdermott *et al.*, 2007; Gordo *et al.*, 2008) although it is a critical factor in deciding among the two methods (annual egg production method AEPM/ Daily egg production method DPEM) used for estimating spawning stock biomass and recruitment process as part of allotting annual fish catch quotas (Hunter *et al.*, 1985; Priede and Watson,

1993; Jennings *et al.*, 2001; Stratoudakis *et al.*, 2006). de Vlaming *et al*. (1982) and Cayre and Laloe (1986) reviewed the use of gonad index to study spawning dynamics. Ovarian growth from about 1% or less of body weight to 20% or more prior to spawning has been reported (Wiegand, 1996).

2.2.5. Fecundity: The estimation of fecundity usually refers to the determination of number of vitellogenic oocytes (potential fecundity), which is strongly influenced by female size, trade-off between egg size and egg numbers, reproductive strategy and spawning pattern of the species (Lambert, 2008). Although fecundity is described as the number of eggs per female, various terms defining the different facets of fecundity exist such as 1) Total fecundity- defined as the standing stock of yolked oocytes at any time; 2) Batch fecundity - the number of eggs in the most advanced stage in a mature ovary ; 3) Annual population fecundity- number of eggs that all females in a population spawn in a breeding season (Hunter *et al.*, 1992; Bagenal, 1978). Fecundity has been related to fish length as well as condition factor (Blaxter and Hempel, 1963; Bengston *et al.*, 1987; Marshall *et al.,* 1998; Oskarsson *et al.*, 2002). Kjesbu *et al.* (1998) reported on the fecundity, egg size and atresia of captive Atlantic cod in relation to proximate body composition while Bleil and Oeberst (2005) studied the variations in potential fecundity of the Baltic Sea cod during the period 1993 - 1999 and found it related to the stock size. Fecundity variations within and between various wild populations of Chinook salmon was reported by Healey and Heard (1984). Thrush and Bromage (1991) reported relationships between fecundity, egg size, egg volume and fish weight in farmed Atlantic salmon.

Classical stock-recruitment models such as Ricker (1954) and Beverton and Holt (1957) take into consideration only stock biomass while efficiency of spawners is generally not taken into consideration (Trippel *et al.*, 1997). However, several studies (Blaxter and Hempel, 1963; Marteinsdottir and Steinarsson, 1998; Vallin and Nissling, 2000) have also indicated maternal influence on egg production both in quantity as well as quality which has important implications for subsequent recruitment to the fishery and its success. Some studies have emphasized that it is the older, larger females which contribute a relatively greater proportion of the population's total egg production and therefore the importance of retention of the brooder fish stock to prevent recruitment overfishing (Hunter and Leong, 1981; Parrish *et al.*, 1986). Larger females which have certain advantages for obtaining food like wider food niche, higher agility in catching prey and also escaping from predators are reportedly placed favorably *vis-à-vis* the smaller females in producing more oocytes through more number of batches of eggs during the spawning season (Chambers and Walwood, 1996; Dominguez-Petit and Saborido – Rey, 2009). Hence inclusion of age/size composition of female fish in the stock for assessing stock recruitment relationships (Marteinsdottir and Thorarinnson, 1998) has been suggested. On the other hand, Ciechomskii and Capezaani (1969) have observed large differences in fecundity of similar sized specimens of Argentinean mackerel *Scomber japonicus marplatensis* while Morgan *et al.* (2007) concluded that the importance of age composition of the spawning stock may not be a universal phenomenon and species to species assessments are required.

Fecundity modality of many multiple spawning species has been assessed using stage specific variations of oocyte size frequency distribution, seasonal decline in total fecundity, seasonal increase/decrease in the mean diameter of advanced vitellogenic oocytes and incidence of atresia (Murua *et al.*, 1998; Macchi *et al*., 2000, 2004; Lapthikhovsky *et al.,* 2002; Plaza *et al.,* 2002; Gordo *et al.*, 2008). Fecundity estimates combined with estimates of abundance of eggs in the sea have been used to estimate the stock biomass of several temperate water species with a single well defined spawning peak (Armstrong *et al.*, 2001). Fecundity estimate in multiple spawning fishes with asynchronous ovary depends on the number of batches of eggs and the fecundity of each batch (Hunter and Goldberg, 1980; Clarke, 1987). In indeterminate multiple spawners, new batches of eggs mature throughout the season and therefore fecundity cannot be reliably estimated from counts of oocyte standing crop nor the number of batches per year deduced from the number of oocyte modes and incidence of post-ovulatory follicles or hydrated eggs also needs to be estimated (Hunter and Goldberg, 1980; Hunter and Leong, 1981; Blaxter and Hunter, 1982). Inter-year variability in relative fecundity in the order of 10 to 20% has been demonstrated for several species of fishes such as *Scomber scombrus* (Walsh *et al.,* 1990) and Plaice *Pleuronectes platessa* (Rjindsorp, 1991).

According to Bagenal (1966) the amount of food available which in turn is related to population density is the most important factor in determining fecundity of the plaice *Pleuronectes platessa*. Yamada *et al.* (1998) reported that batch fecundity of chub mackerel was affected by the nutritional state of spawning

female. Several studies have concluded that when food resources are abundant the reproductive output of adult fish increase due to energy surplus (Hislop *et al*., 1978; Wooton,1979; Townshend and Wootton, 1984; Holdway and Beamish, 1985; Lambert *et al*., 2000). The study by Hay and Brett (1988) indicated that in herrings, during poor feeding conditions, females allocate more energy to the ovaries in relation to body weight than during good feeding conditions. Wootton (1985) observed that in the stickle back *Gasterosteus aculeatus*, that once spawning was initiated the number of batches of eggs produced depended on the food intake. Changes in food availability and *El nino* events are reported to have adversely impacted the fecundity of several multiple spawners such as sardines, anchovies and sprats (Alheit, 1989).

2.2.6. Egg size and Fecundity: Oocyte size measurement have been used to estimate fecundity (Hunter *et al.,* 1985) as well as time to start of spawning (Kjesbu *et al.,* 1994; Oskarsson *et al.*, 2002) and later during spawning, proportion of eggs spawned and spawning frequency (Kjesbu *et al.,*1990). Cayre and Laloe (1986) have stated that ovarian maturation is a complex process and attempting to describe it by a single parameter (eg., oocyte size) however precise can be misleading. Eenennam and Doroshov (1998) have observed that among the various sturgeon (*Acipenser*) species, the Atlantic sturgeon *A. oxyrinchus* has lower egg diameter and approximate individual and relative fecundity almost double at similar body size indicating species-specific characteristics. Chambers and Walwood (1996) could not find any correlation between female size and egg diameter but related to the condition factor K. Egg size is an important

determinant of egg and larval survival (Bagarinao and Chua, 1986; Brooks *et al.*, 1997; Kamler, 1992, 2005) and many authors have reported positive correlation between egg size and fish (deMartini and Fountain, 1981; Eenennaam and Doroshov, 1998). Greater size of larvae from larger eggs have been recorded in several fishes which positively influences their growth and survival and variations (interspecific and intraspecific) in egg size in fishes and its ecological implications have been reported (Ware, 1975). Offspring properties related to egg size is based mainly on two indices, namely, growth and survival, as predation on fish larvae is operating in a size dependant way and the broader feeding spectra of larger larvae which have a larger mouth gape (Knutsen and Tilseth, 1985) allowing better feeding and growth. According to Kjesbu *et al.* (1998) variations in relative fecundities, vitellogenic oocyte distribution and mean size were reflecting a delicate reproductive tactic to minimize negative nutritional effects on egg size and quality under natural environmental conditions. According to de Vlaming (1983) ovulation and spawning are separate events under different control mechanisms and that in the absence of direct observations on spawning females, it is difficult to predict the number of spawnings and number of eggs spawned from oocyte size frequency distribution alone.

2.2.7. Atresia: Follicular atresia is a degenerative process by which oocytes in various stages of their growth and differentiation are lost from the fish ovary (Forberg, 1982; Hunter and Macewicz, 1985; Guraya, 1993). The course of oogenesis in fishes is regulated by environmental, endocrinological and metabolic factors and atresia is considered as an adaptation which leads to

temporary suspension of breeding activity under unfavorable environmental factors (Guraya, 1993). It is an important phenomenon regulating fecundity in many fish species including determinate and indeterminate multiple spawners with low atresia levels characteristic of fishes with determinate fecundity *vis-a – vis* indeterminate fecundity (Macer, 1974; Hunter and Macewicz, 1985; Kjesbu *et al.*, 1991; Witthames and Greer Walker, 1995; Rideout *et al.*, 2000; Murua and Saborido-Rey, 2003). Kjesbu *et al.* (1991) found that actual fecundity decreased by 20 to 80% compared to potential fecundity due to atresia in Atlantic cod. Aleekseev *et al.* (1989) noted that in the flying fishes (*Exocetus* spp.) of the available oocytes only about 75% is contributing to the potential fecundity while the rest is resorbed. Research conducted on rates of atresia based on starvation in captive northern anchovy *Engraulis mordax* along with rates of recommencement of spawning after resuming feeding provides insight into relationships between feeding, somatic energy reserves and egg production (Hunter and Macewicz, 1985).

2.2.8. Whole Oocyte staging and Histology: The macroscopic staging of fish gonads determined from its gross anatomy and microscopic examination of whole oocytes (Clark, 1934; de Jong, 1940; June, 1953; Davis and West, 1993; Smith and Walker, 2004) is a rapid and inexpensive method to determine reproductive status in fishes and routinely done in most fisheries monitoring programmes. However, it lacks consistency especially with regards to certain maturity stages which are difficult to discriminate macroscopically and only histological studies allow precise unambiguous grading and determination of

reproductive status (West, 1990). Hence the use of histological criteria to establish the stages has been recommended (West, 1990). According to Schaefer (1998) the inadequacy of gonad indices/ oocyte diameters for separating developing ovaries in a stage of early vitellogenesis from post-spawning ovaries in atretic stages of resorption is addressed only by histology. Thus it has often been proposed that histologically validated maturity scales be developed at least for those species of major commercial importance that are regularly monitored for fisheries management purposes (James and Baragi, 1980; West, 1990). Accordingly several important commercial species (capelin *Mallotus villosus*- Forberg, 1982; Sea bass *Dicentrarchus labrax* – Mayer *et al*., 1988; Dover sole *Microstomus pacificus* - Hunter *et al.*, 1992; Atlantic sturgeon *Acipenser oxyrinchus*- Eenennaam and Doroshov, 1998; Tilapia *Tilapia zilli* - Coward and Bromage, 1998; Baltic cod *Gadus morhua*- Tomkiewicz *et al.*, 2003; bluefin tuna-Corriero *et al.*, 2003; carp *Cyprinus carpio* - Smith and Walker, 2004; Kathirvelu *et al.*, 2003; Japanese anchovy *Engraulis japonicus* - Funamoto *et al.*, 2004; Argentine hake *Merluccius hubbsi*, Macchi *et al.*, 2004; swordfish *Xiphias gladius* –Arocha, 2002; Poisson and Fauvel, 2009; European anchovy- Ferreri *et al*., 2009) have therefore been assessed using histological aids. Studies by James and Baragi (1980) have indicated that although many marine fishes in Indian waters are multiple spawners, individual species differ in their maturation patterns and more studies to recognize and classify these stages are required possibly employing histological methods. However, relatively few species of

marine fishes of commercial importance have been evaluated using histological indices (Tessy, 1994; Gopalakrishnan, 1991; Rao and Krishnan, 2009).

2.2.9. Studies on Reproduction dynamics of Scombroids: Murua and Saborido-Rey (2003) described the reproductive strategies of a large number of commercially important fishes of the North Atlantic including scombroids such as Atlantic and Chub mackerel, yellowfin tuna and swordfish taking into consideration oocyte development, ovary organization, recruitment of oocytes and spawning pattern. Studies on scombroids (Albacore tuna- Otsu and Uchida, 1959; Atlantic mackerel, *Scomber scombrus* – Morse, 1980; King Mackerel, *Scomberomorus cavalla*- Finucane *et al.*, 1986; Yellowfin tuna- *Thunnus albacares*– McPherson, 1991; Schaefer, 1996 ; bluefin tuna-*Thunnus thynnus*- Medina *et al.*, 2002; Corriero *et al.*, 2003; swordfish *Xiphias gladius*, deMartini *et al.*, 2000; Arocha, 2002; Young *et al.*, 2003; Poisson and Fauvel, 2009) throw light on the general reproductive strategies of these species.

The Indian mackerel which is a scombroid fish is a heterosexual species which does not exhibit sexual dimorphism. Abnormality in gonads of Indian mackerel has only been rarely reported (Prabhu and AntonyRaja, 1959; Rao, 1962; AntonyRaja and Bande, 1972). According to Yohannan (1979) rapid gonadal growth at the expense of somatic growth occurs when the mackerel attains a length of about 21 cm or around 8 months of age. Pradhan and Palekar (1956) developed a maturity scale for mackerel, describing seven stages based on the external appearance of the gonads, its size relative to the abdominal cavity and the range of ova diameter readings in the ovaries. Subsequent

authors have made modifications to this scale by adding further sub-stages (Rao, 1967). However, it is recognized that well-defined maturity scales with fewer stages are preferable over scales that distinguish a larger number of maturity stages (Qasim, 1973; Gerritsen and McGrath, 2006; Costa, 2009). There is no description of atresia in mackerel although incidence of same reported in another pelagic multiple spawning fish the oil sardine, *Sardinella longiceps* (Antony Raja, 1964, 1971).

Devanesan and John (1940) initiated the study of maturation and spawning of mackerel who estimated the number of ripe eggs in the mackerel ovary. Subsequent studies by Pradhan (1956) and Yohannan (1995) also indicated prolonged and batch spawning of the species. Devanesan and John (1940) estimated a fecundity of 94, 000 eggs for *R. kanagurta* while Antony Raja and Bande (1972) estimated it at 37,200 eggs. Shekaran (1958) concluded that the mackerel is a batch spawner where ova are ripened and released in batches but did not mention fecundity as he could not conclude whether after spawning the most advanced batch of eggs the remaining degenerated or proceeded to ripen. Yohannan and Abdurahiman (1998) found mature spawners of the Indian mackerel with hydrated oocytes in gillnets operated at dusk but total absence of such catches in trawls operated during the daytime and concluded it to be indicative of maximum spawning activity in the night.

The ova-diameter frequency method has been most commonly applied to understand the spawning dynamics and fecundity of Indian mackerel (Prabhu and Antony Raja, 1959; Rao, 1962; Radhakrishnan, 1965; Vijayaraghavan,

1962). Yohannan and Abdurahiman (1998) considered the fecundity estimates made by all previous workers an underestimate because of its multiple batch spawning nature. In formalin preserved gonads ova diameter measurements in the range 0.6 – 0.75mm (Prabhu and Antony Raja, 1959; Rao, 1962) and fresh ova measuring 0.6 – 1.071mm (Antony Raja and Bande, 1972) have been recorded. Joseph (1963) noticed shrinkage in tuna eggs preserved in Gilson's fluid. Antony Raja and Bande (1972) noted shrinkage of of 17 and 22% in ripe and maturing mackerel eggs respectively.

2.3. Materials and Methods

The mackerel samples were collected on a weekly basis from mackerel landings by ring seine and trawl nets at various landing centers such as Kalamukku / Cochin Fisheries Harbour and a monthly sample from Alleppey landing center during the period 2005 –2008. The fishing grounds by these ringseine/trawl fishing units are along the Central Kerala coast.

2.3.1.Gonad staging: Freshly caught fish samples were transported to the lab in ice and individual fish were examined for the following: Total length (mm), total weight (gm), maturity stage (immature, maturing, ripe and spent) was recorded which was based on macroscopic observations of the gonad such as the size of ovary/testes in relation to abdominal cavity and its appearance (whether bulging, half shrunk or flaccid; the presence of blood vessels on the ovary and colouration of the gonads) which was primarily based on the maturity scale developed for mackerel by Pradhan and Palekar (1956). Indeterminate stages were recorded separately. Only females were used to prepare a modified key for visual staging

of gonads using macroscopic and histological criteria as ovary is more indicative of spawning activity because females invest more energy into the reproduction process and generally only the female reproductive parameters are considered in stock assessment models (King, 1995; West, 1990) while male gonads were assigned scales based on macroscopic observations only. Maturation pattern was assessed from macroscopic gonad staging of the fish samples collected weekly and pooled over the months during all the years (2005 -2008). Only female gonads in various maturity stages randomly selected from the monthly samples were fixed in 10% formalin for histological studies later.

2.3.2. Gonado-somatic index (GSI): This was calculated for each maturity stage of both sexes using gonads in fresh condition collected during the year 2005 and 2006, by the equation given by Cailliet *et al.* (1986) as:

GSI = Weight of gonads (g) /body weight (g)*100.

2.3.3. Length at first maturity (L_m): This estimate corresponding to size at which 50% of the population attains maturity was estimated for all the years (2005 -2008) by the method given by Udupa (1986) as:

$$Log_{10} m = X_k + X / 2 - (X \sum pi) ,$$

Where, X_k = last log size at which 100% of fish are fully mature

X=log size increment and p_i = proportion of fully mature fish in the i^{th} size group and the L_m (M) = antilog (m).

2.3.4. Ova diameter: The oocyte size frequency distribution of maturing, ripe and spent gonads (stage 4, 5 and 6a &b as per the classification of Pradhan and

Palekar, 1956) was taken after sufficient hardening of the formalin preserved ovaries, usually after 5 – 7 days, using a microscope with ocular micrometer. From the monthly samples, a few ovaries randomly selected were used for detailed studies. Ova diameter of 30 to 100 numbers of oocytes from various ovaries in the different maturity stages were taken along the longest axis to obtain the oocyte diameter frequency distribution following Clark (1934). Oocyte diameter frequency of individual fishes in the various maturity stages were pooled and smoothed using a 3 point moving average to obtain the characteristic oocyte distribution in each maturity stage.

2.3.6. Histology : Representative gonads in various stages of maturity were also assessed using histology to understand the oocyte development patterns. Transverse sections of the selected ovaries preserved in formalin (1:3 tissue : formalin) were washed in running tap water for 5 – 6 hours and then subject to dehydration in ascending concentration of alcohol. Slices of tissue were embedded in Paraplast and histological sections were cut at 5µ. Staining was done with haematoxlyn followed by eosin counterstain (Hunter and Macewicz, 1985).The slides were cleared in xylene and mounted using DPX. Oocytes identified using the description given by Wallace and Selman (1981) were used to understand the oocyte development pattern. Oocyte diameter measurements of each maturity stage were obtained using a digital microscope with image analysis software (Motic BA310). For this only the oocytes sectioned through the nucleus were used (Foucher and Beamish, 1980).

2.3.6. Fecundity: The formalin preserved ovaries collected during 2006 was used for gravimetric analysis of fecundity. The selected ripe ovaries from each monthly sample were washed in tap water, blotted dry and three subsamples of approximately 1mg were taken from the middle of the ovary lobe. All the eggs from each subsample were teased out using fine needles, spread on a glass slide and counted. The Potential fecundity (PF) was estimated as per Bagenal (1978) as

PF= w/W* OW where w = the number of eggs in the sub-sample; W= total weight of sub sample and OW = total weight of the preserved ovaries of the particular specimen.

Relative fecundity was estimated as Potential fecundity divided by body weight (with gonad) as given by Hunter *et al.* (1985). Relation between fecundity and other parameters such as total length, total weight and ovary weight were obtained by fitting data as a scatter plot and fitting linear regressions.

2.4. Results

***2.4.1. Macroscopic gonad staging and Maturity Scale*:** The smallest size at which gonads could be recognized without the aid of microscopy was in the length class > 145 mm. Based on the appearance of the ovary, histological sections and GSI, the mackerel gonads (ovary and testes) could be classified into 4 stages of maturity excluding the indeterminate stage (Tables 2.1 and 2.2; Plate 2.1).

2.4.2. Maturation and spawning: Maturation and spawning appeared as a year round phenomenon. However, peak spawning activity was observed during May-

June and November months along the Central Kerala coast. In all the years of observation, only during the year 2006, the secondary spawning peak usually occurring around November was absent (Fig. 2.1).

2.4.3. Ovary development pattern: Classification of ovaries into four maturity stages using oocyte diameter ranges and GSI values was found to be amenable for routine macroscopic staging studies (Plate 2.1). GSI indicated rapid increase with maturation and these changes were more pronounced in females as compared to males (Figs.2.2 & 2.3). There were 3 modes (300, 550 and 850 µ) in the oocyte diameter distribution of ripe ovaries of which nearly 85% were in the size range of 750 – 1000 µ. The maturing ovary showed a major mode at 450 µ (early stage) and 550 µ (late stage) while the partially spent ovary showed mode at 500 µ (Fig. 2.4)

The oocytes could be classified into four stages of development, namely, perinucleolar oocytes (PN), previtellogenic oocytes (PV), vitellogenic oocytes (VT) and hydrated oocytes (HY) (Fig.2.6., Table 2.3). Ripe ovaries contained predominantly vitellogenic oocytes (Fig. 2.5A) while spent stages were characterized by the presence of previtellogenic oocytes , atretic mature oocytes as well as empty follicles (Fig. 2.5B).

2.4.4. Length at first maturity (L_m) : The L_m varied among the year (2005 - 2008) and ranged from 162 to 196 mm. It did not show any definite trend and was 162, 196, 164 and 174 mm total length during 2005, 2006, 2007 and 2008 respectively (Fig. 2.7).

2.4.6. Fecundity: Total fecundity estimated varied from 10521 to 92279 eggs. Linear regression of fecundity on total length (F= 405.280)*(TL) -59364.6, F=44.58, P <.01, R^2= 0.56) (Fig. 2.8); total weight (F= 5694.14)*(TW) + 2689.9, F= 12.61, P <.01, R^2= 0.3) (Fig. 2.9) and ovary weight (F= 4480.6)*(OW) + 1480.4, F= 41.8, P <.01, R^2= 0.73) indicated strongest relationship with ovary weight followed by total length. Relative fecundity was estimated as 476 ± 163 eggs per gram body weight of mackerel.

Table 2.1. Histologically validated Macroscopic Maturity Scale for female mackerel

Stage	***Description***	***Dominant Oocyte stage (Histology)***	***Mean GSI***
Indeterminate	Gonads tiny and underdeveloped and impossible to differentiate among sex	-	-
Immature (stage F 1)	Gonads small, tubular and pink, oocytes not visible	Previtellogenic	0.38
Maturing (stage F 2)	Gonads tubular, light yellow – orange colouration filling about half of the abdominal cavity. Blood vessels visible on the ovary.	Vitellogenic- lipid droplets appeared, and progressive increase in size and number of lipid droplets	1.26 – 3.98
Ripe (Stage F 3)	Gonads dark orange, turgid and filling the body cavity, transparent ova visible	Vitellogenic -Migratory nucleus stage dominant.	5.10
Spent (Stage F 4)	Gonads flabby with reddish brown gonads.	Post ovulatory follicles (POF), atretic eggs and pre-vitellogenic oocytes	4.00

Table.2.2. Macroscopic Maturity Scale for male mackerel

Stage	***Description***	***Mean GSI***
Immature (M1)	Gonads small, whitish and flattened	0.46
Maturing (M 2)	Gonads pinkish - whitish filling about half of the abdominal cavity.	1.40 (early) – 3.41 (late)
Ripe (M 3)	Gonads white, turgid and filling the body cavity, milt is released on applying pressure	4.61
Spent (M 4)	Gonads flabby with haemorrhagic brownish-white gonads.	2.09

Table 2.3. Oocyte stage classification using oocyte appearance and size range criteria in histology processed ovaries for validation of macroscopic staging

Oocyte stage	***Oocyte appearance***	***Size range***
PN (Perinucleolus)	Oocyte with large nucleus and densely staining cytoplasm.	<10µ
PV (Pre-vitellogenic)	Oocytes with very small lipid droplets in the cytoplasm around the nucleus. Lipid droplets start to form.	120µ-350µ
VT (Vitellogenic)	The zona radiata (ZR) membrane surrounding the oocyte clearly visible. Yolk granules become much more numerous and densely packed. In the later stage some of the lipid droplets coalesce to form large oil globule (migratory nucleus stage).	520µ - 1000µ
HY (Hydrated)	Completely translucent appearance with irregular shape in whole oocyte preparation caused by the fusion of lipid droplets and coalescence of yolk globules to form yolk plates. In histological preparations seen as completely transparent circular shape.	Irregular shape >800 µ

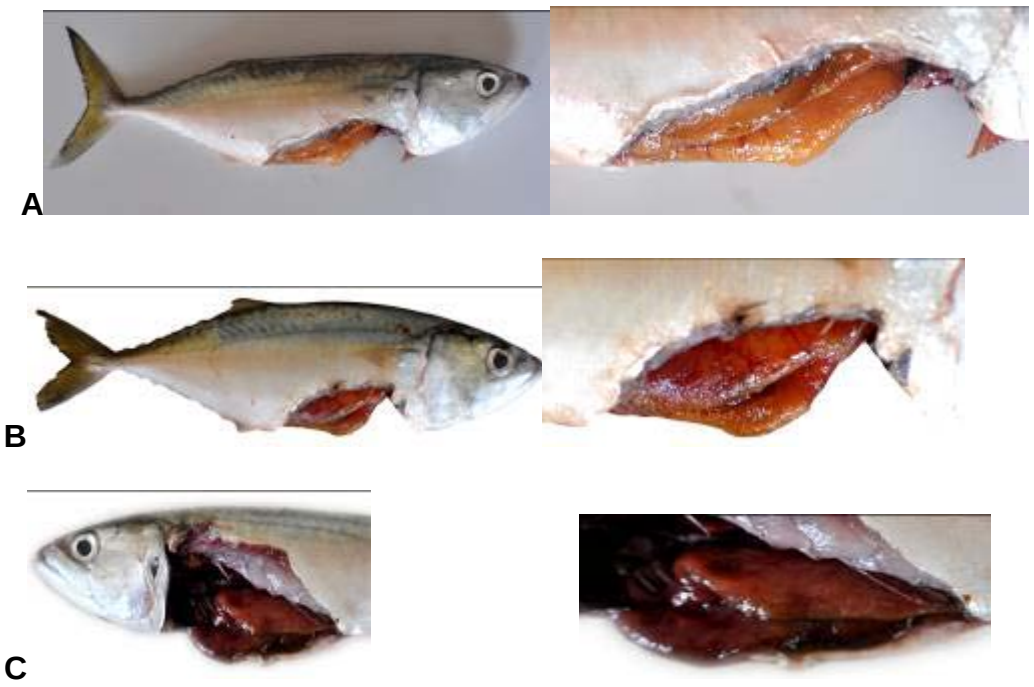


Plate. 3. Macroscopic gonad staging of female mackerel representing A. Maturing (early stage) B. Ripe and C. Spent stages

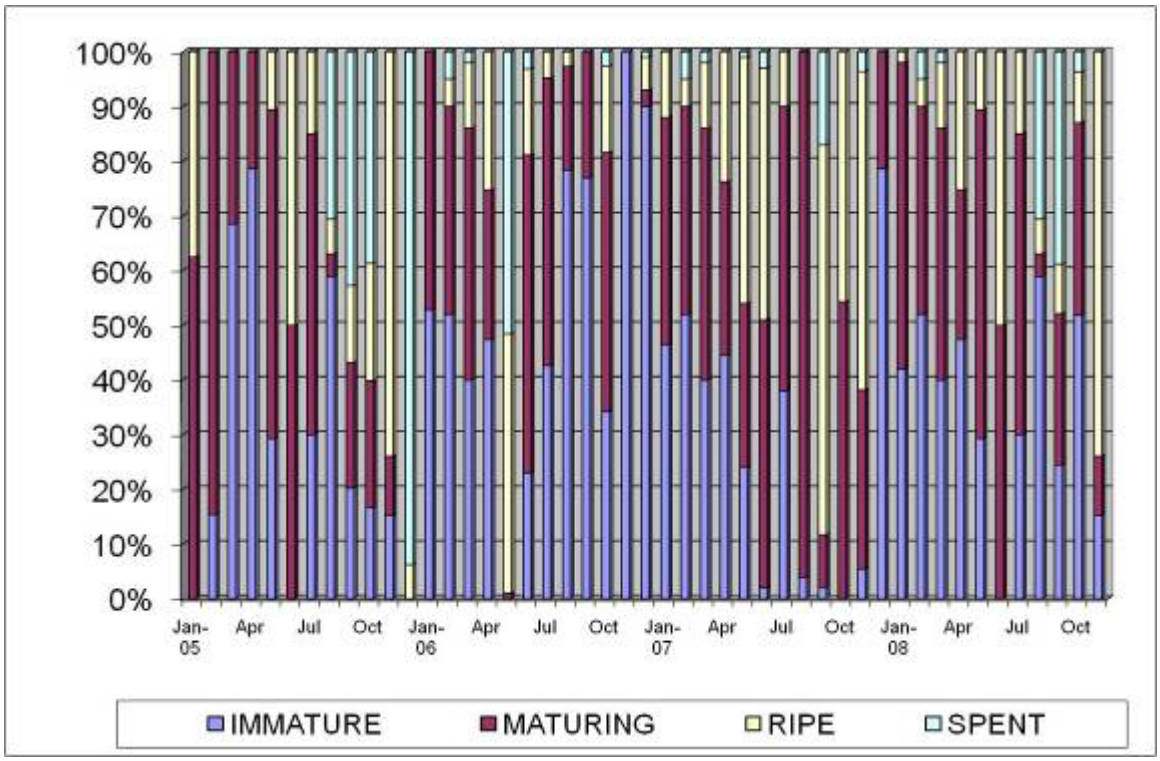


Fig. 2.1. Monthly occurrence of the various maturity stages of *R.kanagurta*

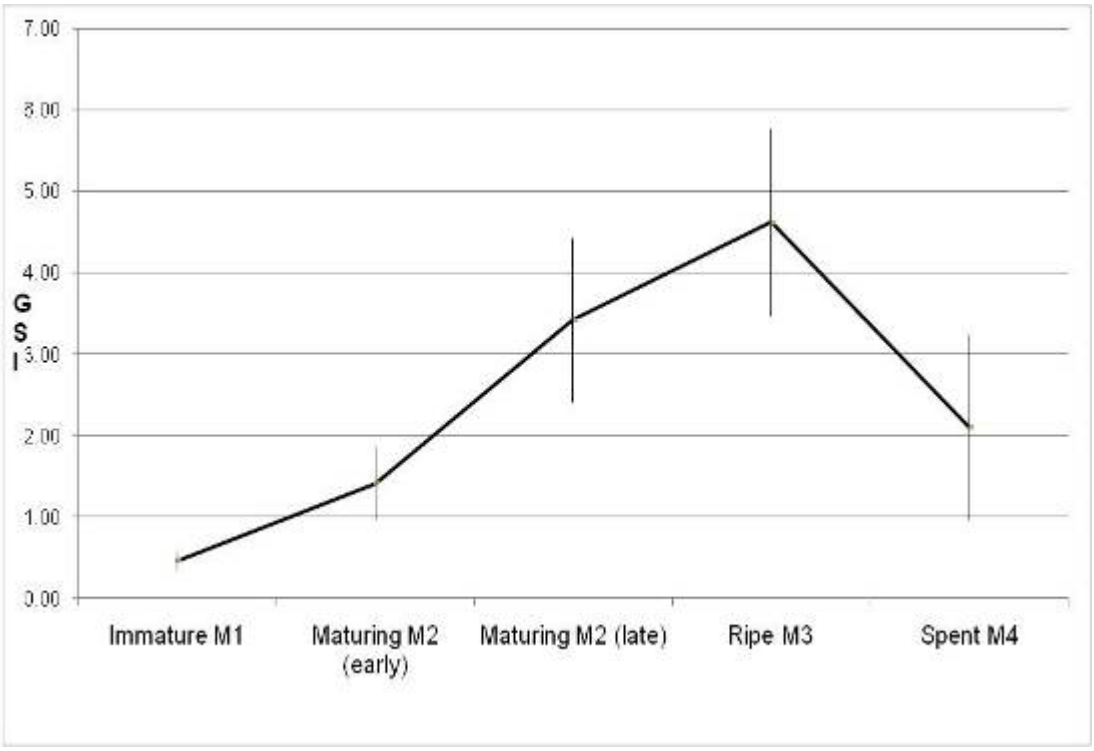


Fig. 2.2. GSI of various maturity stages of male *R.kanagurta* indicating maximum, minimum and mean values (vertical bars)

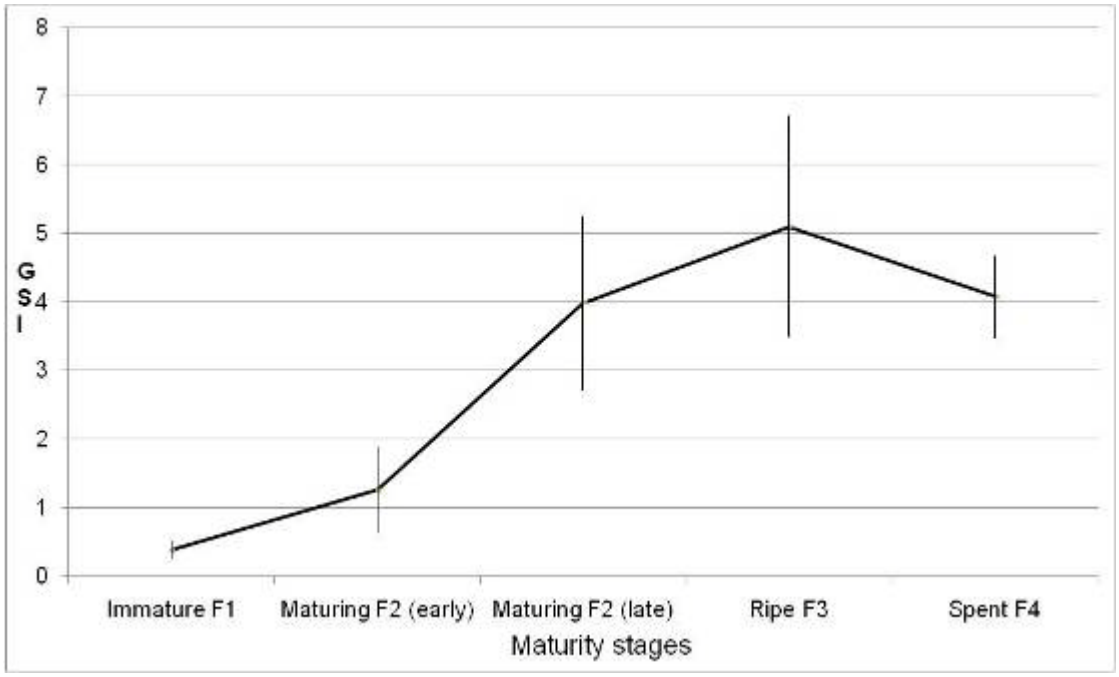


Fig. 2.3. GSI of various maturity stages of female *R.kanagurta* indicating maximum, minimum and mean values (vertical bars)

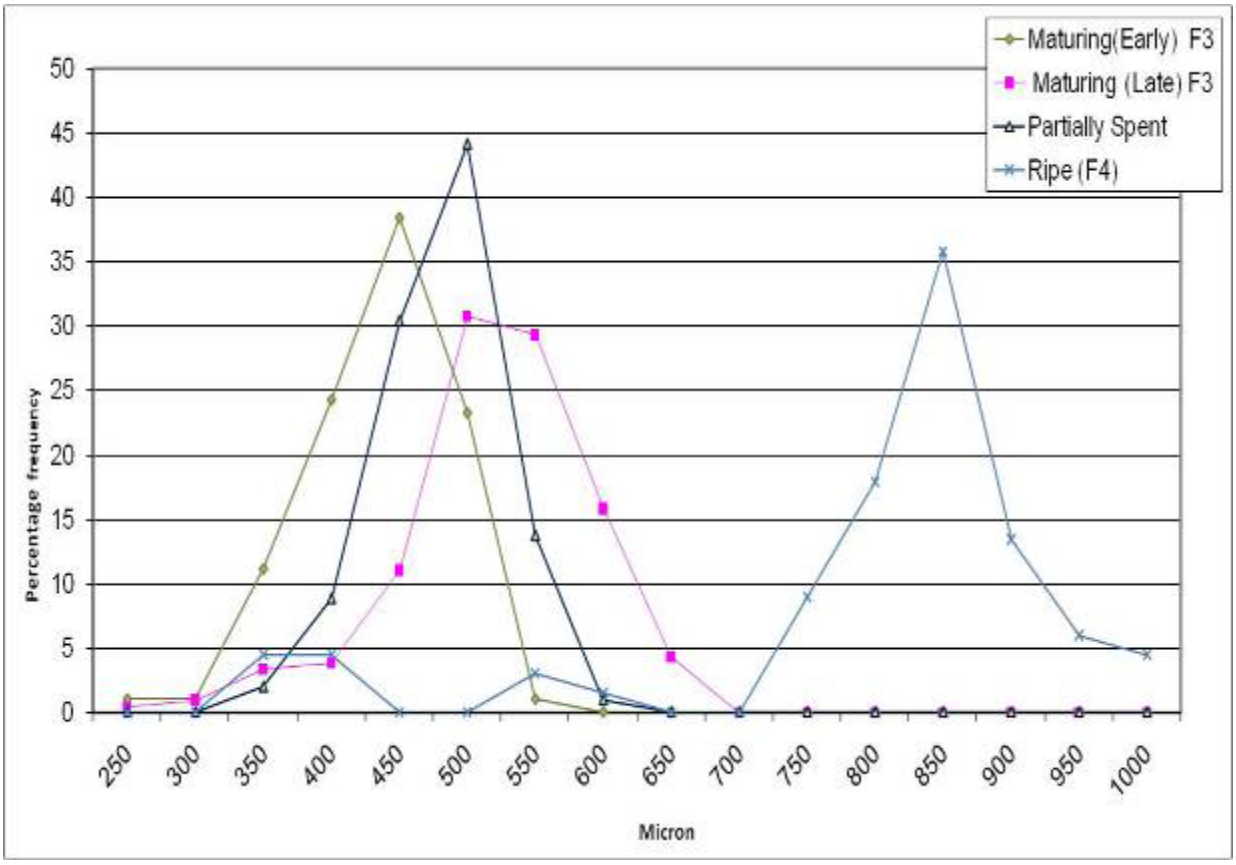


Fig. 2.4. Pooled oocyte diameter frequency distribution of mackerel in Maturing (early) n=16; Maturing (late) n= 14; Ripe (n= 12) and partially spent (n=15) stages. (n = no. of fishes in pooled sample)

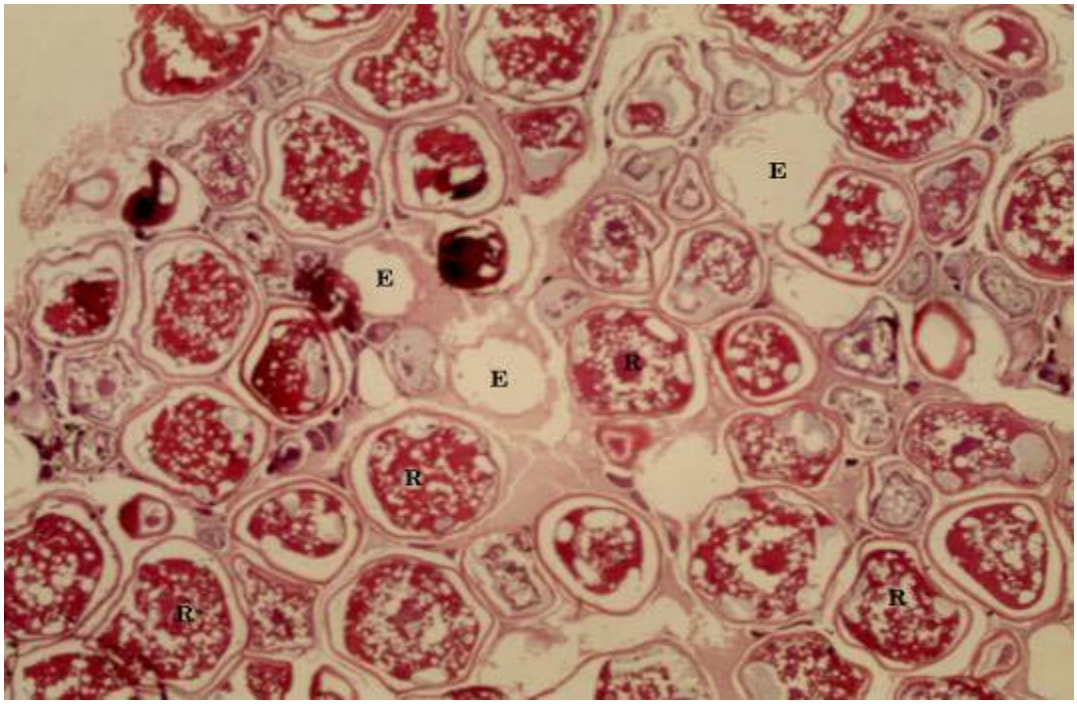


Fig.2.5 A. Ripe ovary (stage F3) with mature oocytes (R) and a few empty follicles (E) indicating ovulated eggs.

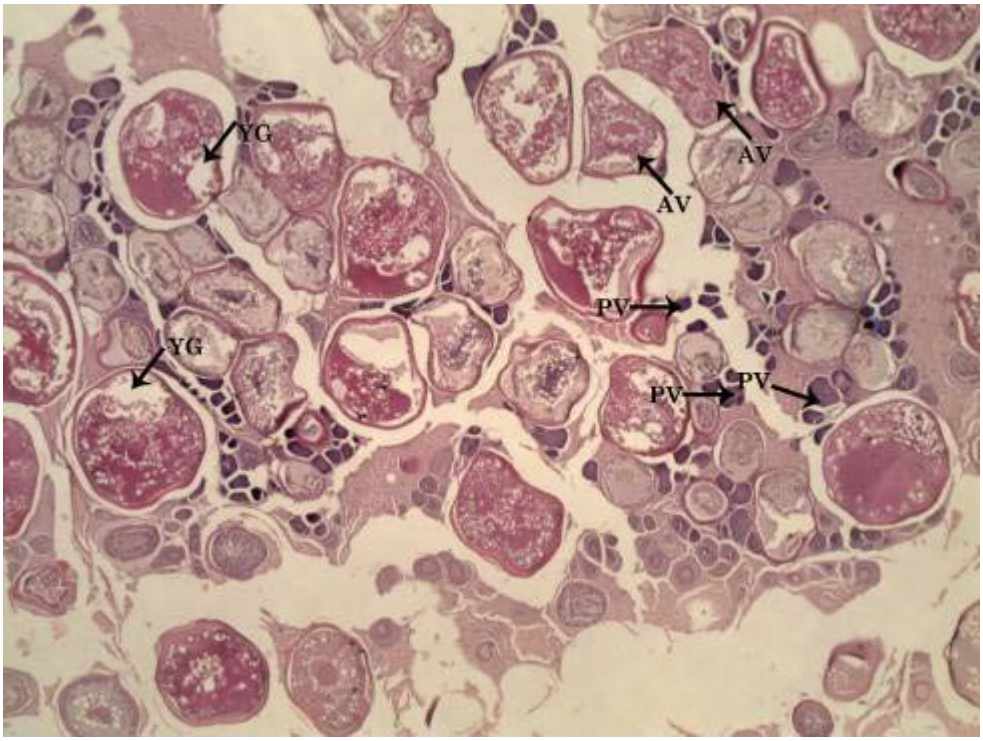


Fig 2.5 B. Spent ovary characterized by very small perinucleolus stage and pre-vitellogenic (PV) stage oocytes and atretic vitellogenic (AV) oocytes

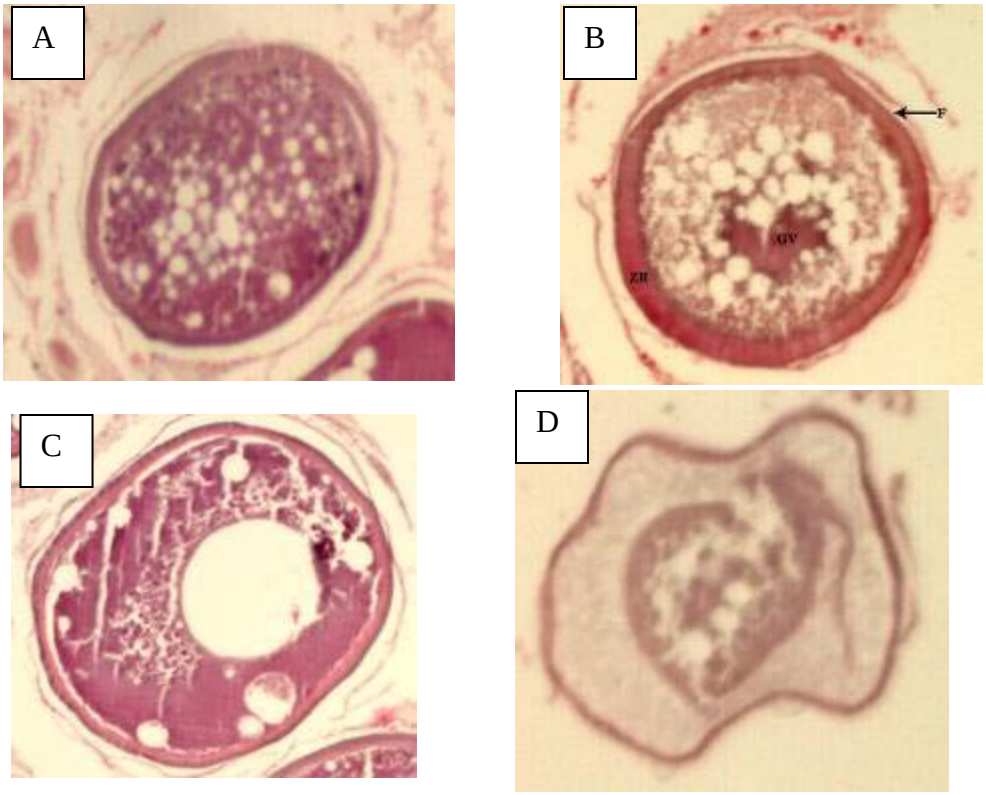


Fig. 2.6. Various stages in oocyte development.

A. Early vitellogenic oocyte with appearance of lipid droplets
B. Oocyte in late vitellogenesis with follicle layer (F), lipid droplets increasing in number and size, zona radiata (ZR) clearly visible and germinal vesicle (GV)
C. Mature oocyte characterized by coalescence of yolk granules and a big lipid droplet
D. Atretic vitellogenic oocyte with irregular shape

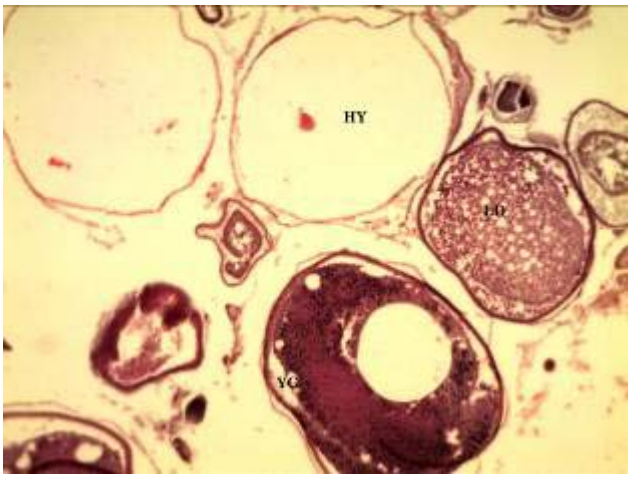


Fig. 2.6a. Characteristic hydrated oocyte (HY) and vitellogenic (LD, YG) oocytes in a ripe ovary

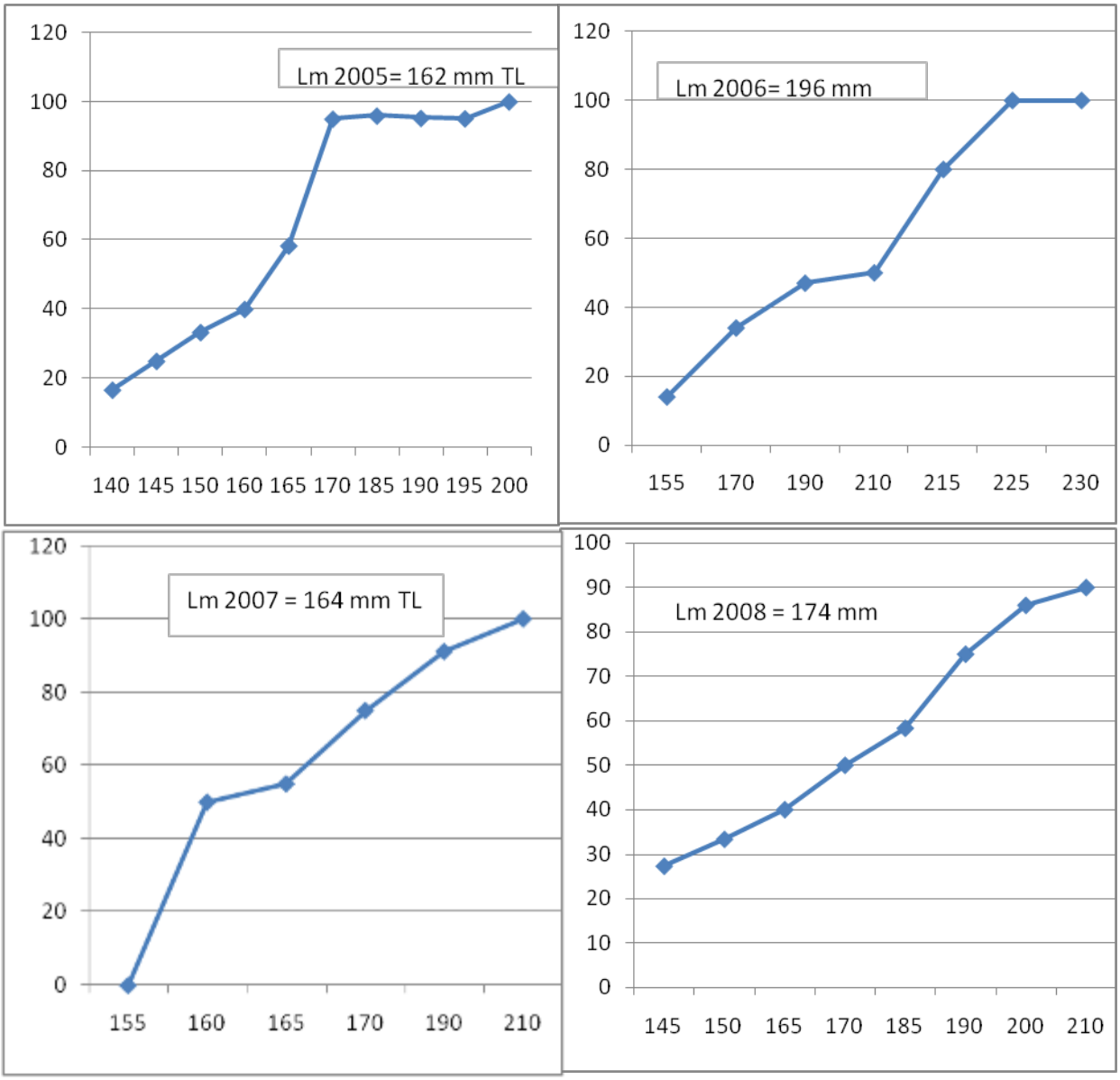


Fig.2.7. Estimated Length at first maturity (L_m) during the different years 2005 to 2008.

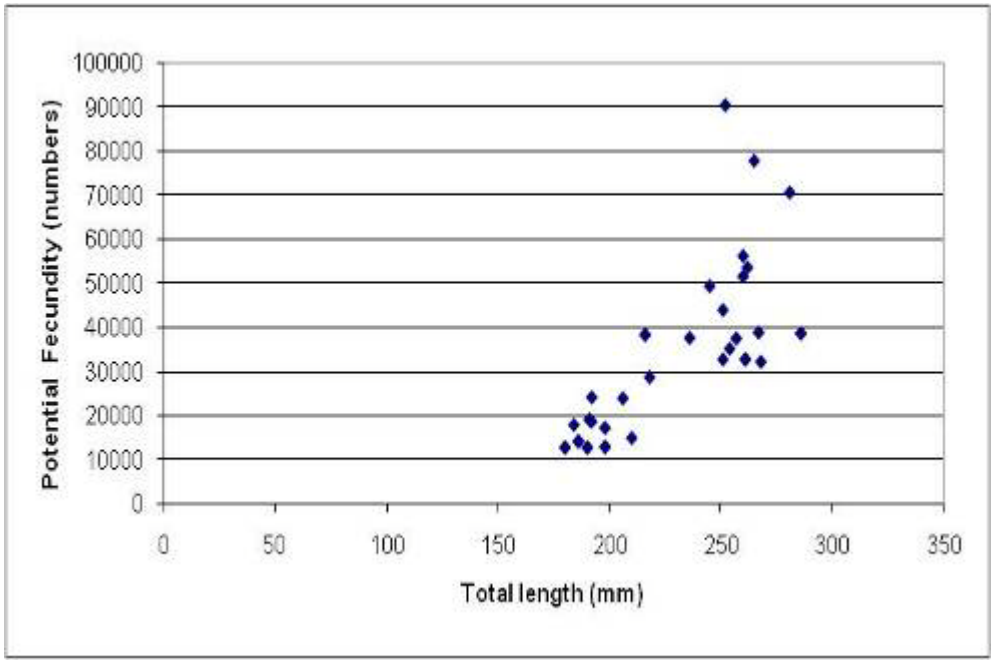


Fig. 2.8. Scatterplot showing relationship of fecundity to total length in *R.kanagurta*

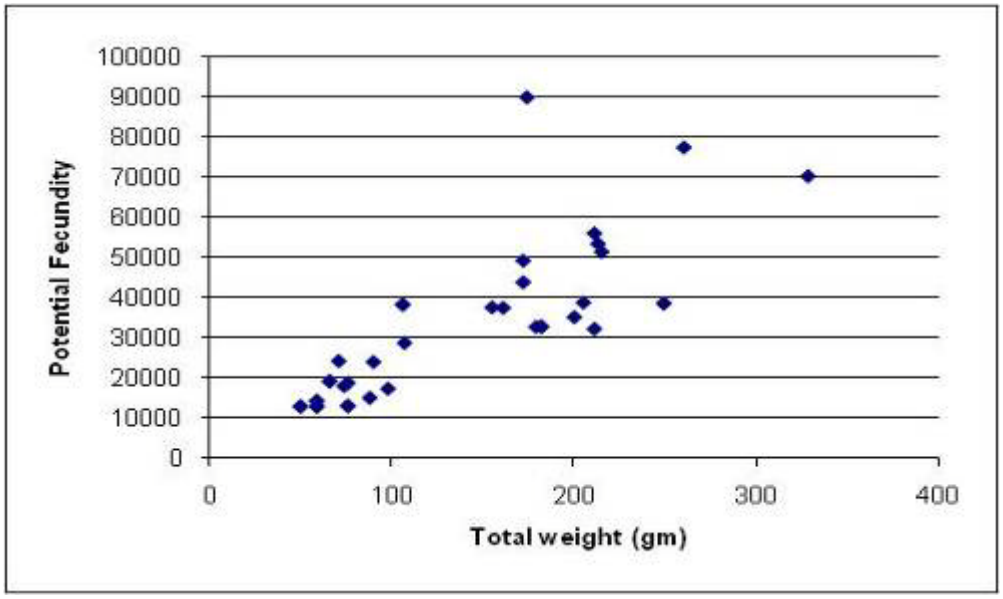


Fig.2.9. Scatterplot showing relationship of fecundity with total weight in *R. kanagurta*

2.5. Discussion

2.5.1. Gonad indices and maturity stages: The gonadosomatic index (GSI) has been used as a measure of maturation in fishes by June (1953). With maturation progressing, the gonadosomatic index (GSI) of mackerel increased more prominently in females than males and could be used as one of the criteria for differentiating among the “maturing” “spent” and the “ripe” maturity stages on a 4 stage scale. The rapid increase in GSI is because of the growth of ovaries due to accumulation of yolk, the nutritional reserve for the embryo, by the oocytes (Wiegand, 1996). Females invest more energy for reproduction compared to males (Henderson *et al.*, 1984) agreeing with the higher GSI values in females compared to males in this study. The final stage of maturation (hydration) could be easily recognized by the presence of translucent ova which is reported to be due to the rapid secretion of a fluid of low specific gravity into the advanced eggs by the granulosa cells of the follicle that causes fusion of the yolk granules resulting in the translucent appearance of the hydrated eggs (deVlaming, 1983; Forberg, 1983). The GSI of a partially spent ovary closely resembled a maturing ovary but could be differentiated by its flabby bloodshot appearance and a narrower oocyte distribution (300 – 550 µ) compared to a ripe ovary which had a broader (250 – 1000 µ) oocyte size range with a definite peak of larger sized oocytes (> 700 µ) clearly separated from oocytes < 500 µ.

The mackerel ovary has been classified into 6 stages with subdivision of stage 6 into 6A, 6B (Pradhan and Palekar, 1956) and even 6C (Rao, 1967) and it basically follows the maturity scale developed for herrings in the temperate

waters by the International Council for the Exploration of the Sea (Holt, 1959). This scale which mainly used gonad appearance and oocyte diameter for maturity stage classification did not find differences in diameter distribution among stages VIA and VIB (Rao, 1972; Yohannan and Abdurahiman, 1998). Similar observations were made in lizardfish (Rao, 1983) also which raises the question for necessity of so many sub-stages. This scale is still being followed for routine macroscopic staging in Indian mackerel as well as several other fishes (Murty, 1983; Sivadas *et al*., 2006; Zacharia and Jayabalan, 2007). Only rarely has maturity classification using fewer stages been attempted as done for the seerfish by Devaraj (1983). The present study confirms the earlier observations regarding ova-diameter distribution in ripe ovaries and also indicates the non-necessity of so many fine stages for the macroscopic staging system. Because the subjective nature of macroscopic judgement of too many fine maturity stages gives rise to lot of variability making comparisons among studies difficult several studies have stressed the importance of simpler but more precisely identified maturation stages fixed using macroscopic as well as histological criteria (Qasim, 1973; Gerritsen and McGrath, 2006; Costa, 2009). Presently there is no histologically validated macroscopic maturity scale for any marine fish of commercial importance from Indian waters for comparison. This simplified 4 scale (immature, maturing, ripe, spent) staging method taking into consideration GSI and oocyte diameter which was validated using histological analysis of representative gonads of the various maturity stages can therefore be evaluated further *vis –a vis* the older maturity scale which consists of 7- 8 stages (Pradhan

and Palekar, 1956) that appears more applicable to temperate water species (Qasim, 1973). Based on this study it is suggested that an ovary with oocytes >750 µ predominant and GSI > 4 can be assigned as “ripe” and uniformly selected for fecundity estimates making comparisons among studies easier .

2.5.2. Maturation and Spawning: The results indicate maturation and spawning to occur throughout the year as witnessed by the occurrence of mature fishes in all the months. However, the main spawning period is during May – June and a minor peak occurs during November as indicated by the consistently higher percentage of mature ones in the monthly landings during the entire period of study. Earlier studies have also indicated high abundance of advanced spawning stages of pelagic fish during May – June along the south west coast of India (Devanesan and Chidambaram, 1948; Pradhan, 1956; Noble, 1974; Anon., 1976; Yohannan and Abdurahiman, 1998a). This study indicates that apparently there has been no major change in the spawning /maturation schedules of Indian mackerel along the southwest coast of India unlike in some other resources such as the threadfin bream (*Nemipterus* spp.) along the Chennai coast which showed shifts in the peak spawning period which was attributed to recent climate-change effects, mainly the increase in sea water temperatures (Vivekanandan, 2009). It is probable that spawning season has remained stable for the Indian mackerel because it is already placed in a favorable environmental window (temperature, salinity) on the west coast as compared to the *Nemipterus* spp. on the east coast which could have taken advantage of the newly formed, more favourable environmental conditions caused by climate-change.

Another possible explanation is that most teleost species exhibit an annual rhythm of breeding largely synchronized or controlled by environmental factors (Lam, 1983; Murty and Vishnudatta, 1976). Thus, the two peak periods of reproductive activity noticed in this study can be said to be coinciding with the monsoon season, when abundant food supply makes it a generally favourable period for larval survival which agrees with observations made by earlier workers (Anon., 1976; Madupratap *et al*., 1994; Yohannan and Abdurahiman, 1998a). Similar conclusions have been drawn by Devaraj *et al*. (1988) and Yohannan and Nair (2002) of a single major brood originating sometime during the February to May period and a secondary smaller brood arising sometime in November that contributes to the mackerel fishery of the west coast of India. The presence of spawners throughout the year but in low percentage compared to the peak spawning season may only be indicating lack of population synchrony in terms of gonad development as noted in other fishes (Rajasilta, 1992; Plaza *et al.*, 2002; Shirashi *et al.*, 2005).

The L_m varied among the years (2005 -2008) and ranged from 162 (2005) to 196 mm (2006) and 164 and 174 mm during 2007 and 2008 respectively showing no particular trend. Earlier workers have reported L_m for the species as 190 - 220 mm (Sekharan,1958; Rao, 1967; Yohannan and Abdurahiman, 1998) while studies conducted during a later period reports it as around 170 mm (Prathibha and Gupta, 2004; Sivadas *et al.*, 2006). The macroscopic staging method which is mostly applied for assessment of L_m has problems while differentiating among post-spawning and early vitellogenic stages and therefore

Hunter *et al.* (1992) recommends caution when differences between maturity studies are observed especially when done by different people, or with different methods or when sampling at different times of the year. The effect of such operator errors, if any, in the estimation of L_m is unknown. Nevertheless, independent studies during two different periods, namely prior to 1980s and during the late 90s by different authors have come to similar conclusions, with studies during the latter period all reporting slight lowering in L_m (Prathibha and Gupta, 2004; Sivadas *et al.*, 2006). The present study shows inter-annual variations but is closer to estimates during the latter period indicates that analysis of historic data may be relevant. This is important because population density- dependant effects on L_m has been reported (Adams, 1980; Helser and Almeida, 1997; Silva *et al*., 2006). Incidentally, peak catches of *R. kanagurta* were made during the 1989 – 1999 period (annual catches of 2-2.8 lakh tons) and there was a significant decline (annual catches of 1 - 1.5 lakh tons) during the 2000 - 2006 period (Yohannan *et al*., 2002; Pillai *et al.* 2007) which are showing slight increase since. This decrease in L_m can be because of less competition for food at reduced population densities which facilitates greater food intake per individual, enabling them to grow fast and achieve maturation at younger ages /sizes as suggested by Jorgensen (1990). Therefore, if any stock dependant mechanisms may be operating is to be looked into with historic data over a longer period of time.

Another point which can also effect the L_m which has to be considered is the role of environmental factors. Changes in L_m has been attributed to changes

in water temperature and resulting changes in habitat preferences and species distribution patterns (Helsel and Almeida, 1997) which is similar to the shifts in distribution and abundance that is being reported in the Indian mackerel recently due to rising sea water temperature and climate-change effects (Asokan *et al*., 2009). Antony Raja (1964) also has reported that L_m in oil sardine, another pelagic fish, has a close positive relationship with the prevailing ecological conditions during the previous year (oil sardine matures at about 1 year of age, similar to mackerel) when they recruited to the commercial fishery in the immature state. Thus this study indicates that a rigorous analysis of historic databases on the maturity and spawning of Indian mackerel may throw light on the population dynamics of the resource.

2.5.4. Oocyte development and Fecundity: The present study indicated that the mackerel ovary development may be considered group synchronous based on the classification by de Vlaming (1983) where three clutches of oocytes could be distinguished in the ripe stage. This is considered to be the most common type of ovarian development in teleost fishes (de Vlaming ,1983).

In the ripe ovaries, one pronounced batch of advanced vitellogenic oocytes in the size range 0.75 – 1.0 mm with peak at 0.85 mm was observed in this study. This is similar to the earlier reports of Radhakrishnan (1965) who recorded a maximum size of 0.94 mm for ripe ova with modal group between 0.62 and 0.75 mm and Vijayaraghavan (1965) who reported it to be between 0.67 - 0.74 mm. It thus appears that egg size in mackerel does not show much variations over temporal scales and thus oocyte diameter measurements can be

used for making rapid estimates of potential fecundity in mackerel. For this, the oocyte stages validated using histological methods indicated oocytes > 520 µ to be vitellogenic and hence considering that the most advanced clutch in a ripe ovary is > 700 µ, this size can be used as a cut-off point to make rapid estimates of potential fecundity. Egg sizes are reported to be characteristic for various species (Rao, 1962; deVlaming, 1983) and considering that size of mackerel egg is relatively stable, in conjunction with other morphological characters it can even be used for identification of mackerel eggs in the plankton samples.

The observation of nearly 90% of the developing oocytes in the size range of 750-1000 µ with a single mode at 850 µ and a considerable gap with smaller oocytes is indicating a batch spawner with determinate fecundity as classified by Hunter and Goldberg, (1980) and de Vlaming (1983). A distinct hiatus in oocyte size frequency between pre-vitellogenic and vitellogenic oocytes is characteristic of determinate spawners (Hunter *et al.*, 1992; Gordo *et al.*, 2008) as was observed in this study. Similar observations have been reported in the mackerel off Mangalore coast (Rao, 1967) and lizardfish on the east coast (Rao, 1983) (Rao, 1983) of India. However it is in contrast with the pattern of many modes of developing eggs and a single advanced mode observed by Yohannan and Abdurahiman (1998a) in the mackerel population off the Malabar coast which is a distinctive upwelling ecosystem.

It is still unknown how many times the individual fish spawns over an annual cycle as final oocyte maturation (FOM) process in fishes is reported to

proceed in a rather asynchronous fashion first and later after a period of inactivity on favourable environmental cues in synchrony (Mylonas *et al.*, 1997, 1997a; Kathirvelu *et al*., 2003). Therefore to know spawning frequency of mackerel experiments using individual spawners in captivity may have to be taken up. The relatively short peak spawning period of 2-3 months in May-June period, the pronounced peak of mature oocytes in ripe ovaries which contains nearly 90% of the total oocytes and the other modes being such small sized that it may take some time to develop into hydrated oocytes indicate that the possibility of a secondary spawning in the same season is very remote and chances appear to be more in favour of degeneration and resorption than maturation in case of unspawned ova. Antony Raja (1964, 1971a) has also arrived at a similar conclusion for oil sardine, another small pelagic species. Occurrence of atretic vitellogenic oocytes alongwith pre-vitellogenic oocytes in spent mackerel ovaries lend further support to this conclusion. Besides, the length frequency of mackerel catches indicate only two to three well defined broods in the fishery (Rao, 1962; Rao, 1967; Yohannan and Abdurahiman, 1998a; Yohannan *et al*., 2002) which also supports the conclusions drawn in this study . Thus, taking into consideration the well defined peak spawning season and a pattern of determinate fecundity, it should be possible to make reasonable estimates of annual recruitment strength for stock assessment purposes in mackerel along the central Kerala coast.

The number of eggs in ovaries classified as “Ripe” in the present study varied from 39,600 eggs to 73,781 eggs while the relative fecundity was

estimated as 476 ± 163 eggs per gram body weight. Absolute fecundity estimates of mackerel in earlier studies range from 94,000 eggs (Devanesan and John, 1940); 20,911 to 111,000 eggs (Rao, 1967) and about 38,000 eggs (Antony Raja and Bande, 1972). Several workers felt that fecundity of mackerel is much higher than these reports (Sekharan, 1958; Yohannan and Abdurahiman, 1998) though no estimates were given, citing the need for more information on spawning frequency. Because the spawning frequency of each individual has not been studied, the fecundity count in this study only indicates the range of available mature oocytes (absolute fecundity) at the moment of observation only and are within the range reported by earlier studies. Estimations of absolute fecundity in multiple spawner fishes are complicated as there can be biases by factors such as incomplete ovulation (de Vlaming, 1983), effects of previous spawning activity (Plaza *et al.*, 2002), continuous addition of oocytes to stock of mature eggs in indeterminate spawners (Hunter and Goldberg, 1980) and atresia (Macer, 1974). Yet, this study does not indicate much variation in absolute fecundity from those reported by earlier workers. However, the relative fecundity of mackerel estimated in this study is much lower than the range of 701 - 866 eggs reported by Rao (1967) in mackerel off Mangalore coast. It is not clear if any geographical and ecological factors are responsible for these variations as has been reported in certain other fishes (Bagenal, 1966; Silva *et al*., 2006) as no estimates of relative fecundity has been reported by other workers to enable a comparison. Some fishes are known to adjust clutch size in response to proximate environmental conditions such as food availability and

food quality (McDowall and Eldon, 1997) and whether changed environmental conditions such as increased temperature which affects plankton production is affecting fecundity through dietary modulation of reproduction (Masuda, 2009) +in mackerel is yet to be assessed. Taking into consideration above factors, only with direct observations on spawning of mackerel in captivity, or sampling of fish in known spawning grounds in well defined intervals it may be possible to further improve these estimates.

Compared to fecundity estimates (3.66 - 6.88 lakh eggs) of mackerel of the genus *Scomber* (Ciechomski and Capezzani, 1966), fecundity estimates of the Indian mackerel *Rastrelliger kanagurta* are low. The results of the present study also suggest that ovarian weight and total length are most important in determining fecundity of Indian mackerel. Similarly, Johnson (1971) has reported that fecundity and weight of mature ovaries are an exponential function of standard length. The present study indicates that in mackerel larger sized fish can produce more eggs which is in contrast with the observations of Schaefer (1998) who noticed high variation in batch fecundity estimates in similar sized yellow fin tuna, which is another scombroid fish. However, several studies have noted a linear relationship between fecundity and fish length (James and Vasudevappa, 1978; Coates, 1988). Thus the observations in the present study are pertinent for the implementation of length-based fishery management measures. Presently more emphasis is placed on conservation of juveniles and a minimum legal size (MLS) of around 160 mm to ensure that mackerel can spawn at least once (Yohannan and Nair, 2002; Pillai *et a*l., 2009). Considering that

fecundity is related to its length, it would be profitable to evaluate the impacts of conserving spawners in the larger size range of 230-270 mm as indicated by this study.

To summarise, the life span of mackerel is less than two years (Devaraj *et al*., 1998) and its life history traits such as relatively short life span, small size at maturity, multiple spawnings are in all probability aimed at maximizing reproductive output within its life span as pointed out by Tyler and Dunn (1976). High inter-annual variations in recruitment and catches of mackerel has been observed. As the present study indicates fecundity of Indian mackerel may be limited by its size but nutritional condition which plays a major role in the reproductive success of wild fish populations (Lambert *et al*., 2000) may also be another important factor. Gonad development is to a large extent dependant on food energy (Lambert and Dutil, 1998; Darriba *et al*., 2005) and hence studies on the feeding dynamics of mackerel are also very pertinent to assess the diet preferences and variations in utilization of food resources as the fishes grow through their lifecycle to mature, reproduce and recruit to the fishery, which is addressed in the following chapter.

****

CHAPTER 3
FOOD AND FEEDING DYNAMICS

CHAPTER 3

FOOD AND FEEDING DYNAMICS

3.1. Introduction

Food intake is the major factor controlling fish production. Quantitative assessment of food habits in fishes is therefore an important aspect of fisheries management and a study of food and feeding of fishes can shed light on the behaviour, habitat use, energy intake of the various fish species and inter / intraspecific interactions that occur in the aquatic ecosystem (Walters *et al.,* 1997). The diet of fishes changes with a number of factors which are extrinsic (biotope, region) or intrinsic (species, size, behaviour) and thus information on diet of fishes is important to understand the basic functioning of fish assemblages which are important for developing Ecosystem Based Fisheries Management (EBFM) models (Hanson and Chouinard, 2002; Kublicki *et al.,* 2005). The concept of “critical feeding period” has been found to be useful in understanding the variations in recruitment of wild fish stocks (Keast *et al.,* 1985) and also an understanding of how the various fish species utilize available food resources allows identification of factors that affect their distribution and abundance (Ellis and Musick, 2007). In the aquaculture sector also, broodstock nutrition plays a critical role in the reproductive performance of many fish species (Bromage and Roberts, 1995; Brooks *et al.,* 1997; Iziquierdo *et al.,* 2001).

The Indian mackerel is an important fishery resource in the Indian EEZ especially along the southwest coast of India as well as an important forage item for the highly valued food fishes such as seerfishes and tunas occupying higher trophic levels (Vivekanandan *et al*., 2009). During the 90s there was a dramatic

increase in catches of Indian mackerel along the Kerala coast due to introduction of an innovative fishing gear, the ring seine but over the next few years catches showed decline and remained low until the mid-half of this decade (Pillai *et al*., 2007). Recently, climate-change induced impacts such as extension of its distribution range and increasing catches along the north-west coast of India is also reported (Asokan *et al.,* 2009). According to Link and Garrison (2002) although it is debatable whether food type or quantity influences spawning, fecundity, juvenile survival and consequent recruitment to the fishery, understanding the feeding preferences in relation to physiological cycles, prey availability and population dynamics will be an important step that can throw light on the ecosystem dynamics and responses of fish stocks to human perturbations. Most studies of food and feeding habits of mackerel are at local scales, mostly from the Malabar upwelling ecosystem in the northern part of Kerala or the Karnataka coast and in scattered time periods especially during the 60s and 70s (Noble and Geetha, 1992). These studies have reported mainly only on the occurrence of the various food items in the gut contents. Hence a more detailed study of the feeding ecology of mackerel along the central Kerala coast in conjunction with studies on maturation and lipid dynamics was attempted.

3.2. Review of Literature

3.2.1. Fish diet studies: As food intake is the major factor controlling fish production, studies of food intake and growth of the various species is expected to yield valuable information for assessing the role of the particular species in the marine food web, predator- prey interactions and production efficiency which can

be usefully employed in developing EBFM models (Walters *et al*., 1997; Gascuel *et al.,* 2005). Qualitative (diet composition), semi-quantitative (prey proportions) and quantitative (consumption rates) information can be got from fish stomach content datasets (Berg, 1979; de Crespin *et al.,* 2000). When combined with information about rates of evacuation, diet information can be used in assessments of the total food consumed by fish populations (Durbin *et al.,* 1983; Penczak, 1985; Vivekanandan, 2001).

Diet composition studies are thus an integral part of EBFM models which require knowledge on energy transfer and species interactions through the food web (Langton, 1982; Penczak *et al.,* 1984; Walters *et al.,* 1997; Garrison and Link, 2000). Most studies on fish diets rely on examination of stomach content to quantify prey abundance usually to a coarse taxonomic resolution where the main aim of the study is ecology-based (Robichaud *et al.,* 1991; Liao *et al.,* 2001; Hovde *et al*., 2002; Griffiths *et al.,* 2007).

Several methods have been proposed to study fish diet, which has been reviewed by Hyslop (1980), Pillay (1952) and Windell and Bowen (1978). Traditional indices used for stomach content analysis which include percent composition by number (Ni), weight/volume (Wi or Vi) and frequency of prey occurrence (Oi); the stomach fullness index (SFI) and the Points method where food items are awarded points proportional to their estimated contribution to stomach volume (Hynes 1950; Pillay, 1952) as well as modifications of the standard methods (Natarajan and Jhingran, 1962; Pinkas *et al.,* 1971; Fritz, 1974; Strauss, 1979; Jensen, 1980;Wallace, 1981; Mohan and Sankaran 1988;

Costello, 1990; Cortes, 1997; de Crespin *et al.,* 2000; Lima and Goltein, 2001) are still widely used to evaluate diet of various fish species. The usage of compound indices which combine two or more diet measures into a single index such as the Index of Relative Importance (IRI) (Cortes, 1997) has been criticized for providing little or no additional information than that provided by single indices (Macdonald and Green, 1983; Hansson, 1998).

Qasim (1972) while providing a critical appraisal of the existing knowledge of food and feeding habits of marine fishes in Indian waters, emphasized the importance of chemical analyses of food of fishes as it is of crucial importance in understanding dynamics of energy and its chanelling to various trophic levels. Qasim and Jacob (1972) studied diet of fishes such as oil sardine, mackerel and mullet in terms of energy units as determined by organic carbon content while Salonen *et al.* (1976) studied the relation of energy and organic carbon in aquatic invertebrates. Sterner and George (2000) investigated the carbon, nitrogen and phosphorous levels in whole fish and gut samples of several cyprinid species and used it to build nutrient flux models. Assessment of nutritional benefits of feeding in fishes through analysis of stomach contents has been expressed in bio-energetic terms (Probst *et al.,* 1984; Keast and Eadie, 1985; Cunjak and Power, 1987) while stable isotope analysis of fish gut contents have been made to arrive at a time-integrated diet picture that also aided understanding of energy transfer in marine food webs (Sholto-Douglas *et al.,* 1991; Hesselsein *et al.,* 1993; Monteiro *et al.,* 1991; Zanden *et al.,* 2001; Yoshi *et al.,* 1999). Promising new techniques such as fatty acid tracers have also been used to understand trophic

ecology of the various ecosystems incorporating fatty acid analysis of tissues of the various animals in the ecosystem which are either prey and/or predators (Iverson *et al.,* 2002).

Feeding habits of several coastal marine fishes of India (Venkataraman, 1960; Qasim, 1972; Jacob and Rajagopal, 1980; Vivekanandan *et al.,* 2009) have been reported. Feeding habits of scombroids which includes the Indian mackerel have been reported (coastal species of tunas- Kumaran, 1962; spanish mackerel, *Scomberomorus* spp.– Vijayaraghavan, 1955; Jenkins *et al.,* 1984; bullet tuna *Auxis rochei*- Mostardo *et al*, 2007; mackerel tuna *Euthynnus affinis*- Griffiths *et al.,* 2009). From Indian waters most of the studies on food have described only qualitative/quantitative aspects of diet composition (Qasim, 1972) and studies to estimate food consumption and production efficiency of the wild fish stocks are very few (Devaraj, 1999; Vivekanandan, 2001).

3.2.2. Food resources and their nutritive value: Kublicki *et al.* (2005) noted that biotope complexity and home range of the species is a significant factor affecting the variability of prey items observed in fishes. Rating and comparing of prey taxa in the diets of fish on an importance scale is based on the assumption that some taxa are more important than others to the growth, survival, recruitment, size structure, condition, reproductive success or other aspects of the ecology of the predator species (Liao *et al.,* 2001). Invertebrate prey are reported to provide the highest food quality in terms of both protein and energy compared to the primary food resources of algae, macrophytes and detritus (Bowen *et al.,* 1995; Persson, 1983). However, detritus based food webs are also

important in planktonic marine systems and it has been hypothesized that more phytoplankton carbon is probably processed by detritus pathways than by grazing pathways (Pomeroy, 1980; Bowen, 1984). Microbes are reported to make detrital carbon available to animals and play an essential part in overcoming the nitrogen deficiency of detritus (Mann, 1988). According to Newell (1984) the role of bacteria as a potential food resource for higher trophic levels in the marine pelagic systems is as important as phytoplankton to herbivores, especially when they are associated with aggregated particulate material and can be retained by the filtration structures of larger consumer organisms. The utilization of dissolved organic matter (DOM) from the plants through its physicochemical precipitation as amorphous particulate organic matter (POM) which is utilized by finfishes and shellfishes has been well documented in freshwater environments (Bowen, 1981). On the other hand, marine phytoplankton such as diatoms, dinoflagellates and other algae are very important sources of polyunsaturated fatty acids such as docosahexaenoic acid (DHA), eicosapentaenoic acid (EPA) and arachidonic acid (AA) which is passed on to copepods, fishes and other higher trophic levels through the marine food chain (Tocher, 2003).

3.2.3. Seasonal and Ontogenetic diet shifts: Ontogenetic diet shifts which are linked to maximizing energy inputs have been noted in several species of teleosts, elasmobranchs and crustaceans (Lowe *et al.,* 1996- tiger shark *Galeocerdo cuvier*; crayfish *Procambrus clarkia*- Correia, 2002; Houde *et al*., 2002 halibut *Reinhardtius hippoglossoides*; Galarowicz *et al.,* 2006- walleye

Sander vitreus; McElroy *et al.,* 2006- sandbar shark *Carcharhinus plumberus*; Graham *et al*., 2007- yellow fin tuna *Thunnus albacares*; Mahe *et al.,* 2007- Hake *Merluccius merluccius*).Various reasons have been attributed to the observed shifts such as, (i) seasonal variations in the availability of the prey types; (ii) size related shifts in morphological factors such as an increased mouth gape size of the predator and its agility and (iii) habitat shifts caused variations in foraging ground selected by the predator during its life cycle driven primarily by its inherent behaviour (Winemiller, 1989; Schaefer *et al.,* 2002; Szedlmayer and Lee, 2004; Figueirido *et al.,* 2005; Graham *et al.,* 2007; Mahe *et al.,* 2007). In the ontogenetic diet shifts associated during larval to juvenile phases, mouth size, development of swimming abilities and increased visual sensitivity are believed to play important roles (Blaxter, 1986; Kawakami and Tachihara, 2005) while in diet shifts associated with habitat shifts, availability and ease of capture of the different prey items play a key role (Szedlmayer and Lee, 2004). Ontogenetic changes in foraging patterns have also been linked to prey profitability which has significant impact on growth processes and population dynamics in fishes (Galarowicz *et al.,* 2006).

Several studies have also indicated seasonal variation in diet composition of fishes (Labropoulou *et al.,* 1997; Flavia *et al.,* 2000; Link and Garrison, 2002; Sever *et al.,* 2005). The importance for predators that shift diet to synchronize their lives with fluctuations in resource availability such as pulses of new cohorts of prey fish/ zooplankton / phytoplankton blooms was highlighted by Persson and Bronmark (2002). According to Link and Garrison (2002) the major determinants

of cod diet as a hierarchical sequence are, firstly, cod size which determines what can be eaten, secondly, preference for specific prey and third, abundance of all available prey.

3.2.4. Feeding dynamics and maturation: Feeding has been observed to reduce during maturing in certain fishes which is attributed to the body cavity being smaller just prior to spawning with ovaries filling the body cavity (Milton *et al.,* 1994) while in certain other species active feeding is reported during the gonad maturation process also (Hynes, 1950; Krishnamoorthi, 1971; Goncalves and Almada, 1997). In those species where maturing fish are observed to become anorexic indicates that final stages of gonadal growth are dependant on energy reserves (Jorgensen *et al.,* 1997) whereas increased feeding during maturation and spawning indicate energy needs are largely met by increased dietary intake and not depending on body reserves (Hasek and Felder, 2006). Selective predation on larger high energy prey by maturing fish which enables them to continue to grow rapidly while developing gonads has been reported (Milton *et al.,* 1994). The costs of parental care in teleosts and ways in which males and females differ in their investment of energy resource in reproduction has been studied (Childress *et al*., 1980; Miller, 1984; Henderson *et al.,* 1984; Jonsson *et al*., 1991; Goncalves and Almada, 1997). Clarke and Holmes (1986) reported that variations in lipid content and composition with sex and season in mid-water decapods was mostly influenced by the pattern of food availability. Food dependant variation in stored lipid energy has been found to influence the reproductive potential of individual fish (Rajasilta, 1992; Milton *et al.,* 1994;

Henderson *et al.,* 1996; Henderson and Wong, 1998; Yamada *et al.*,1998) and at stock level found to constrain recruitment (Barents sea cod - Marshall *et al.,* 1999; chub mackerel- Yamada *et al.*, 1998). Wootton (1977) studied the effect of food limitation on the size, body components and egg production in stickle back *Gasterosteus aculeatus*. Wooton (1979) opined that when food resources are abundant the reproductive output of adult fish increased due to energy surplus.

3.2.5. Diet of Indian Mackerel: Studies on food and feeding of mackerel have been done through periodical examination of stomach contents and indicated a planktonic diet with dominance of copepods and presence of diatoms, dinophysids, crustaceans, molluscan larvae, algae, amphipods and miscellaneous items (Bhimachar and George, 1952; Pradhan,1956; Rao and Rao,1957; Noble, 1962; Venkataraman and Mukundan, 1970; Sivadas and Bhaskaran, 2008). Rao (1962) indicated a primarily planktivorous diet for mackerel but varying depending on the exigiencies of the environment to include detritus and bottom algae also. Devanesan and Chidambaram (1948) suggested that the mackerel supplements its planktonic diet with dead and decaying fishes while according to Kuthalingam (1956) mackerel is piscivorous. However piscivory has not been observed in fishes caught along the east coast (Rao, 1962; Luther, 1973) compared to studies on the west coast (Kuthalingam, 1956; Kutty, 1965; Sivadas and Bhaskaran, 2008). Selectivity in feeding habits has been attributed to the Indian mackerel by some workers (Bhimachar and George, 1952; Pradhan, 1956). Madhupratap *et al.* (1994) concluded that in species such as mackerel spawning may be occurring in inshore waters with abundant food

but the microbial loop of the food chain is likely to be important in determining the maternal effects on egg quality especially in those years with weak / episodic monsoon upwelling and which probably acts as a safety valve with regards to recruitment of mackerel. Bhimachar and George (1952) reported that in inshore waters the diet of mackerel was dominated by copepods (50%), followed by cladocerans, larval/adult decapods, phytoplankton, lamellibranch larvae and fish eggs/larvae. Rao (1962) studied the food habits of mackerel (24 –32 cm size) from more offshore areas in drift nets operated off Vizhinjam found feeding to be lowest during October to December coinciding with peak spawning activity. Qasim and Jacob (1972) noted that the ratio of body carbon to food carbon in *R.kanagurta* was 1 compared to a ratio of 5-7 in phytoplankton and detritus feeders like oil sardine and mullet. However little information is available on the feeding dynamics of Indian mackerel in relation to maturation and ontogenetic variations, if any.

3.3. Materials and Methods

The mackerel samples were collected weekly from mackerel landings by ring seine and trawl nets during January 2005 to June, 2006 at various landing centers such as Kalamukku / Cochin Fisheries Harbour. The fishing grounds of these fishing units are along the Central Kerala coast. Freshly caught fish samples were transported to the lab in ice and individual fish were evaluated for the following: Total length (mm), total weight (gm), maturity stage (immature, maturing, ripe and spent) and stomach fullness (empty, traces to 1/4 full, 1/2 full, 3/4 full or full). To study the variations in food intake individual fish were cut open

and depending on the state of distension of the stomach were assigned as poorly fed (empty to 1/4 full), moderate (1/2 full) and actively fed (3/4 to full). Qualitative analysis was done using guts of actively fed specimens (almost full (3/4) to full stomachs) which were preserved in 5% formalin with labels indicating all biological details of the individual fish such as length, weight, sex, maturity stage and date of capture.

The formalin preserved actively fed stomachs were cut open and stomach contents were identified into broad but exclusive categories such as copepods, diatoms, dinoflagellates, crustaceans (excluding copepods), foraminifera, tintinnids, fish eggs, chaetognaths, sand and detritus. Fine greenish or brownish coloured organic matter that could not be attributed to any category was classified “detritus” as differentiated from “sand” which had grainy texture. Digested tissue remains probably of fish/shrimps occurring as a whitish pasty mass which could not be identified were classified as “digested”. The frequency of occurrence of each food item was calculated as given by Hynes (1950) as F_i= 100 * N_i / N where F_i is the frequency of occurrence of the i food item in the sample; N_i = number of stomach in which the i^{th} item was found and N= total number of stomachs with food examined.

Percentage volume (% V_i) of each of the various food items was calculated using the Points (volumetric) method as given by Hynes (1950).The Index of Preponderance (I_p) was assessed (Marshall and Elliott , 1997) as given below:

$I_p = (V_i O_i / \sum (V_i O_i) * 100$ where V_i and O_i are percentage volume and occurrence of particular food item i. Percentage Preponderance index (% I_p) was arrived as % $I_p = (I_p / \sum I_p) * 100$

To obtain information on the seasonal diet variations, data was analysed according to seasons which based on ecological characters were classified (Menon *et al*., 2000) as follows – Pre-monsoon (February to May), Monsoon (June to September) and Post- monsoon (October to January). Ontogentic diet variations were studied using a size based classification into 5 size groups such as < 140, 141 – 170, 171 – 200, 201 – 230 and >230 mm taking into consideration its life history where first maturation is reached around 170 - 190mm (Chapter 2). Diet similarities among seasons was compared using Spearman Rank Correlation Coefficient (R_s) as given in Fritz (1974) using 12 prey categories that occurred in all the seasons and excluding “molluscs” and “chaetognaths” which was observed only during the monsoon and post-monsoon seasons respectively. The graphical method of Costello (1990) was used to plot percentage occurrence against percentage volume and relative importance of each item interpreted with respect to the positions in the graph. Diet breadth was calculated for each size group using the formula by Cailliet *et al*., (1986) as given below:

$B = 1/\sum (p_i)2$ where p_i is the proportion of the i^{th} of the N items in the diet.

Food limitations are identical with energy limitations and according to Omori and Ikeda (1984) in the marine food web nutrient transfer can be expressed either in terms of energy, or, of any of the chemical elements (C, H, N) of the animal and even a combination of these two indices. As the elements such as C and N are of dietary origin and indicate the biochemical composition as well as energy storage pattern (Anderson and Pond, 2000) it was studied in relation to maturity stage and diet factors. The energy content of the muscle tissue of mature and ripe stages of male and female mackerel was estimated using a CHN analyzer. For this, 3 individuals of each sex and stage collected during May 2005 were used. The "ripe" stages were differentiated from "mature" stage in having predominantly translucent oocytes in hydrated stage, visible even without the aid of microscopy. Muscle tissue of the specimens was dried in an oven at 60^0 C overnight to remove moisture till constant weight was attained and then ground to fine powder using mortar and pestle. Pre-weighed powder was used for determination of ash content by ashing in muffle furnace (450 ^{0}C for 12 hours). Elemental analysis of Carbon (C), Hydrogen (H) and Nitrogen (N) was done in a CHN elemental analyser Vario ELIII CHNS. The elemental composition data were expressed as ash-free dry weight (AFDW) following the formula given by Gnaiger and Bitterlich (1984) as

$W_c = {}_{tot}W_c - {}_{ash}W_c * W_{ash} / 1 - W_{ash}$ where ${}_{tot}W_c$ is the total carbon mass in the total dry biomass (g total C/g ${}_dW$); ${}_{ash}W_c$ is the inorganic carbon fraction in the ash (g inorganic C/ g_{ash}); and W_{ash} is the mass fraction of ash in the dry weight (g ${}_{ash}$/ g ${}_dW$).

The caloric content was calculated using a formula of Gnaiger and Shick (1985) as given by Ikeda (1996): $(4.436\ W_N + 66.265\ W_C - 11.2)/4.18$ where W_N and W_C are fractions of N and C respectively on an AFDW basis. To supplement these observations, differences if any, in food preferences among sexes was evaluated using a sub-sample of 39 specimens (190 – 240 mm TL size group) having full stomachs collected during April to August 2005, which covered the pre-monsoon and monsoon seasons. The volumetric percentage composition of the prey groups in 21 males and 18 females was analysed using ANOVA in SPSS software.

3.4. Results

3.4.1. Feeding intensity: Empty stomachs were observed throughout the seasons while active feeding was highest during monsoon (Fig. 3.1). Among maturity stages, feeding activity was high even in ripe and spent stages (Fig. 3.2). The feeding intensity declined in the largest size groups (>231 mm) during the monsoon and post-monsoon seasons but in the pre-monsoon season even larger size groups were found to be actively feeding (Fig. 3.3a-c). Among size groups, irrespective of seasons, feeding intensity was highest in the <140 mm size class which abruptly declined in the 141 – 170 mm size class with only poor to moderate feeding activity. Further feeding increased rapidly in the 171 – 230 mm and was most prominent during the post monsoon season (Fig. 3.3 C & D).

3.4.2. Seasonal variations: Most of the food items were present throughout the seasons with copepods and diatoms most commonly observed in the stomachs examined in all the seasons. The frequency of occurrence (F_i) of crustaceans

was highest during monsoon and post-monsoon seasons while foraminifera, algae, sand and detritus were most frequently occurring in the guts during the pre-monsoon season (Table 3.1).

The Preponderance Index (I_p) however indicated differences in proportions of the various prey consumed among the seasons (Table 3.2 & Fig. 3.4.) Detritus ranked first during the pre-monsoon season only while copepods and 'digested matter' complex dominated during the monsoon and post-monsoon period (Table 3.3). Spearman Rank Correlation Coefficent (R_s) indicated no significant differences among the monsoon and post-monsoon seasons but significant differences when compared to the pre-monsoon season (Table 3.4).

Table 3.1: Percentage occurrence (F_i) of various food items during the different seasons

Item/Season	Pre-monsoon	Monsoon	Post-monsoon
Copepods	64.3	89.9	95.3
Diatoms	64.3	69.6	72.1
Dinoflagellates	13.1	30.4	32.6
Fish eggs	10.7	5.1	2.3
Crustaceans	15.5	69.6	44.2
Foraminifera	67.9	25.3	7.0
Tintinnids	16.7	5.1	9.3
Algae	54.8	26.6	34.9
Detritus	78.6	36.7	11.6
Sand	63.1	7.6	9.3
Digested	66.7	100.0	86.0
Molluscs	0.0	7.6	0.0
Chaetognaths	0.0	0.0	11.6
Total	100	100	100

Table 3.2: Percentage Preponderance Index (% I_p) of various food items during the different seasons

Prey items	Pre-monsoon	Monsoon	Post-monsoon	All seasons (combined)
Copepods	16.89	43.86	39.29	33.3
Digested	15.13	28.70	41.48	28.4
Detritus	28.48	1.91	0.82	10.4
Diatoms	8.58	9.47	5.78	7.9
Crustaceans	0.67	12.67	10.45	7.9
Foraminifera	11.87	0.13	0.13	4.0
Algae	8.12	1.54	1.19	3.6
Sand	9.31	0.14	0.02	3.2
Dinoflag	0.29	1.46	0.80	0.9
Tintinnids	0.53	0.03	0.02	0.2
Fish eggs	0.14	0.01	0.01	0.1
Molluscs	0.00	0.10	0.00	0.0

Table 3.3. Ranking based on season-wise Preponderance Index (I_p)

Prey Item/season	Pre-monsoon	Monsoon	Post-monsoon	Average ranking
Detritus	1	5	6	3
Copepods	2	1	2	1
Digested	3	2	1	2
Foraminifera	4	9	8	6
Sand	5	8	9	8
Diatoms	6	4	4	4
Algae	7	6	5	7
Crustaceans	8	3	3	5
Tintinnids	9	11	10	10
Dinoflag	10	7	7	9
Fish eggs	11	11	11	11
Molluscs	12	10	11	11
Chaetognaths	-	-	6	12

Table 3.4. Seasonal variations in diet composition assessed using Spearman's Rank correlation coefficient (R_s)

Season/ R_s	*Pre-monsoon*	*Monsoon*	*Post-monsoon*
Pre-monsoon	1.0	0.482	0.181
Monsoon		1.0	0.778*
Post-monsoon			1.0

*significant correlation

3.4.3. Ontogenetic variations: Among size groups, the Ip indicated dominance of detritus (0.376) followed by copepods (0.193) in the largest (>230 mm) size group. Copepods, diatoms and dinoflagellates predominated in the 171 – 230 mm size range while in < 140 mm size group , "copepods" item (0.622) was dominant followed by digested matter (0.249) (Table 3.5, Fig. 3.5). Diet breadth was highest in the size class > 230 mm indicating more generalized feeding habits compared to < 140 mm size groups (Fig. 3.6).

Table 3.5: Preponderance Index (I_p) for the various size groups of mackerel

Prey/size group (mm)	<140	141 -170	171- 210	211 - 240	>241
Copepods	0.622	0.473	0.704	0.723	0.193
Diatoms	0.129	0.006	0.251	0.104	0.042
Dinoflag	0.000	0.000	0.029	0.064	0.000
Fish eggs	0.000	0.000	0.001	0.000	0.004
Crustaceans	0.000	0.172	0.000	0.008	0.002
Foraminifera	0.000	0.000	0.000	0.001	0.146
Tintinnids	0.000	0.000	0.000	0.004	0.005
Algae	0.000	0.001	0.012	0.008	0.162
Detritus	0.000	0.000	0.004	0.001	0.376
Sand	0.000	0.000	0.000	0.039	0.044
Digested	0.249	0.347	0.000	0.048	0.025

3.4.4. Diet composition and Energy content: Costello Analysis (Fig. 3.7) which indicates the general feeding preferences of the fish indicated copepods and diatoms to be the most important. Diet composition among both sexes indicated copepods, diatoms and digested matter dominant but contribution of crustaceans, algae and detritus was higher in females compared to males (Table 3.6, Fig. 3.8). While no significant differences in energy composition among sexes was observed ($F=.011$, $P > 0.05$) significant differences ($F=31.8$, $P< 0.05$) were observed among the mature and ripe stages within each sex (Fig. 3.9).

Table 3.6. Volumetric diet (% V_i) composition of mackerel (male and female)

Prey item	Females (Vi)	Males (Vi)
Copepods	31.6	41.2
Diatoms	6.1	14.3
Dinoflagellates	1.6	5.8
Fish eggs	0.2	0.0
Crustaceans	21.7	5.2
Foraminifera	0.8	0.0
Tintinnids	0.7	0.2
Algae	7.1	0.8
Detritus	5.9	2.5
Sand	3.0	0.0
Digested	20.2	26.4
Molluscs	1.2	0.9
Chaetognaths	0.0	2.8

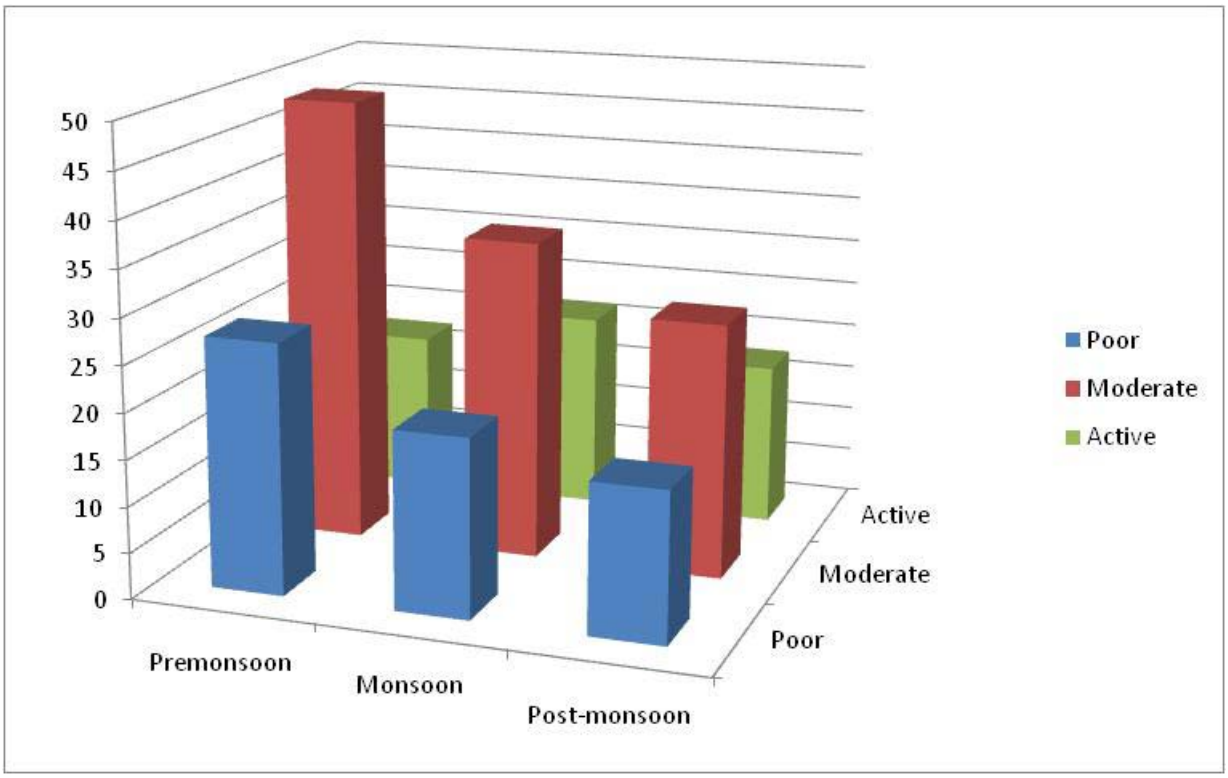


Fig.3.1 Feeding intensity (% numbers) in relation to seasons

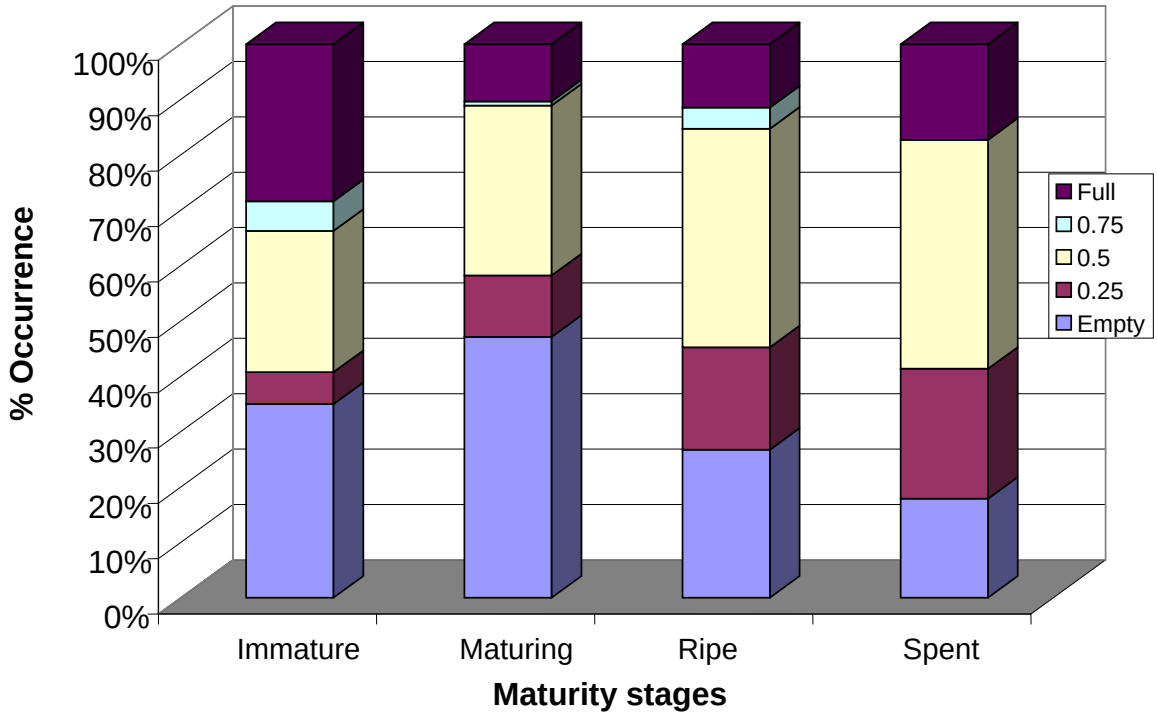


Fig. 3.2. Percentage occurrence of stomachs of various feeding activity in the different maturity stages

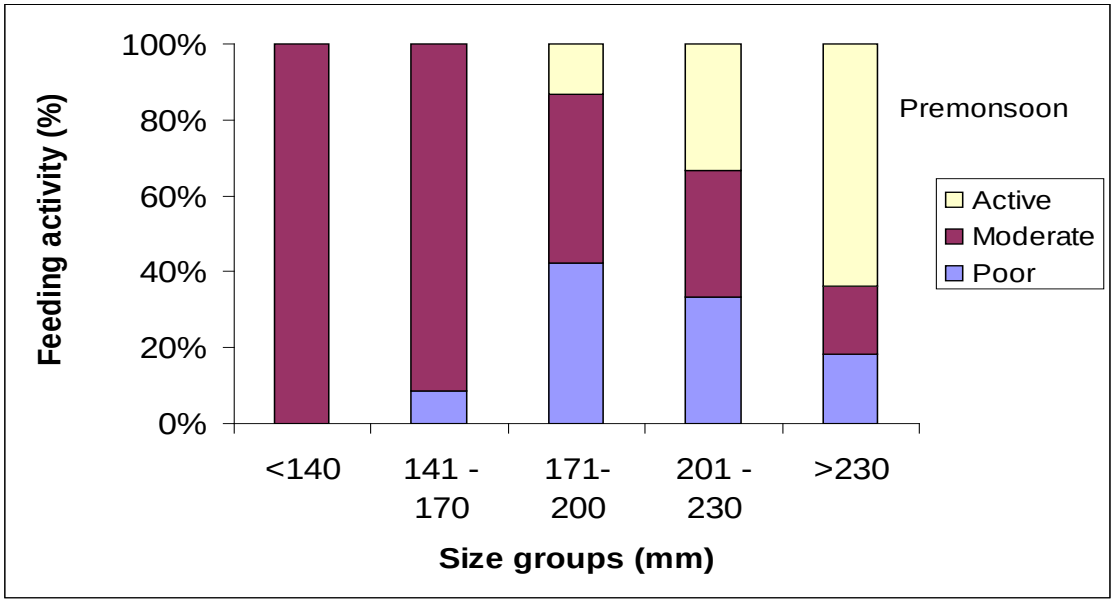


Fig. 3.3 A. Size-based feeding activity during pre-monsoon season

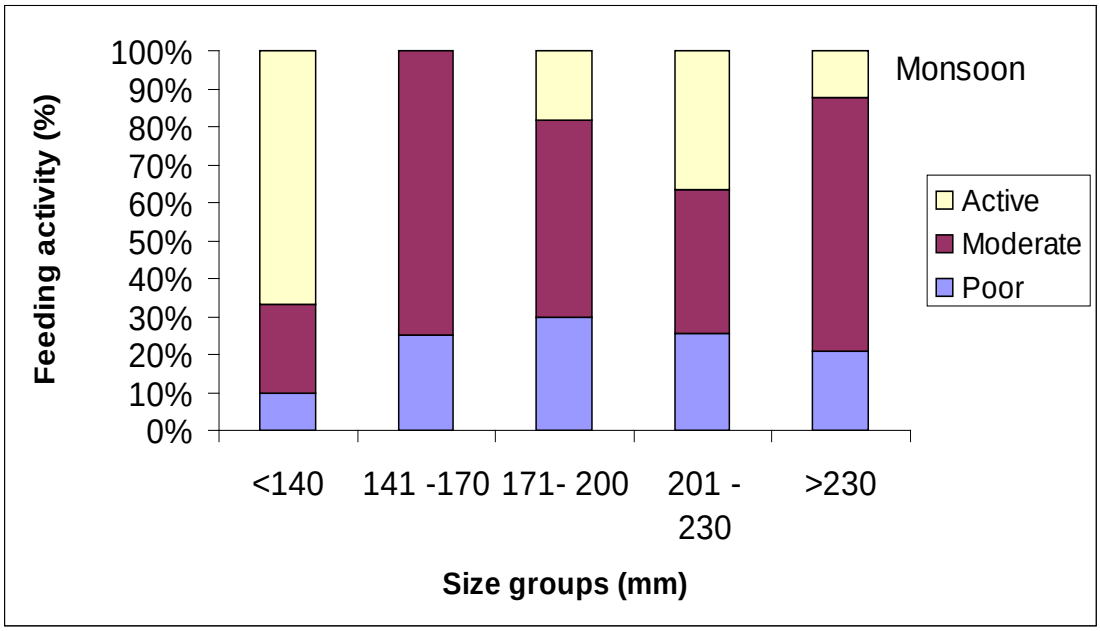


Fig. 3.3 B. Size-based feeding activity during monsoon season

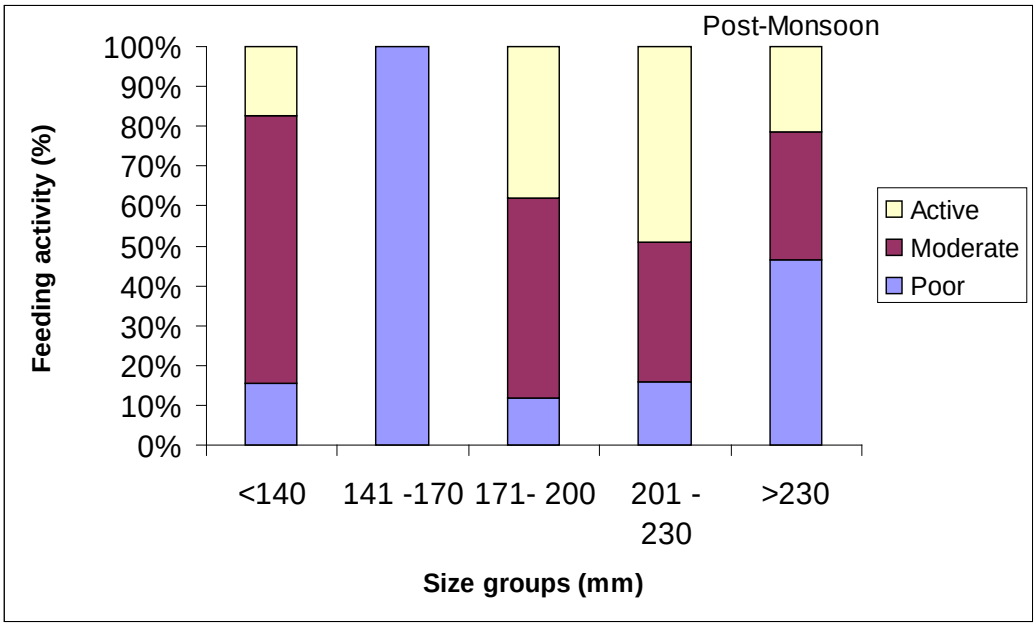


Fig. 3.3 C. Size-based feeding activity during post monsoon season

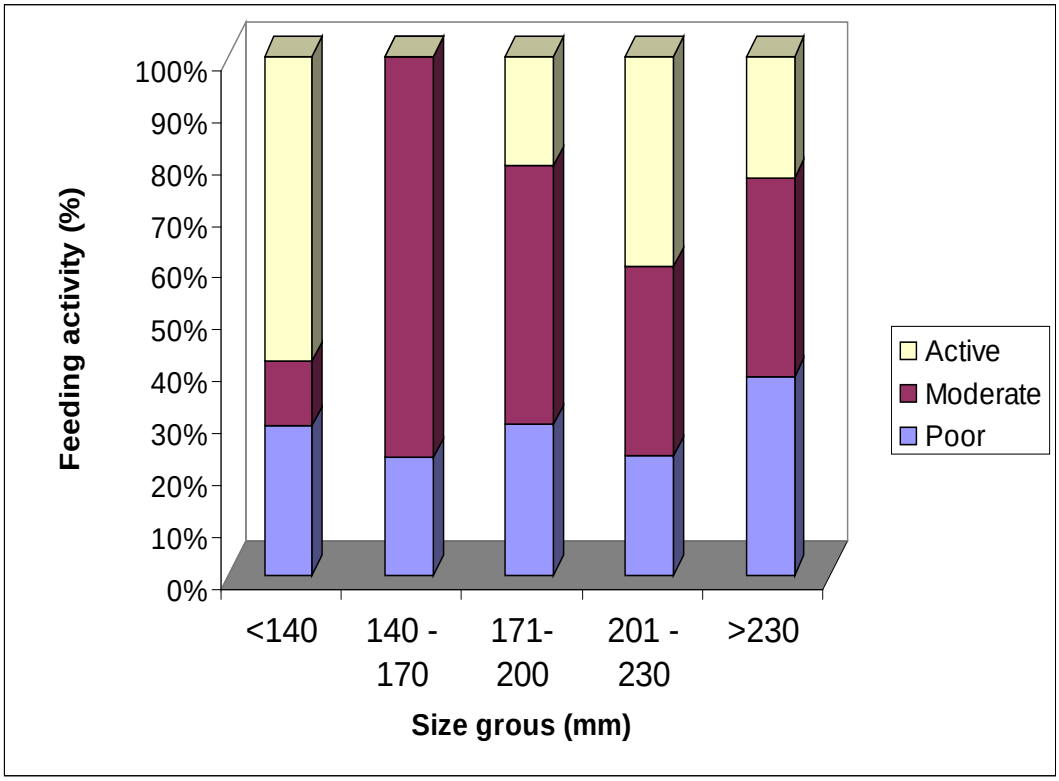


Fig 3.3 D. Size- based feeding activity combined for all seasons

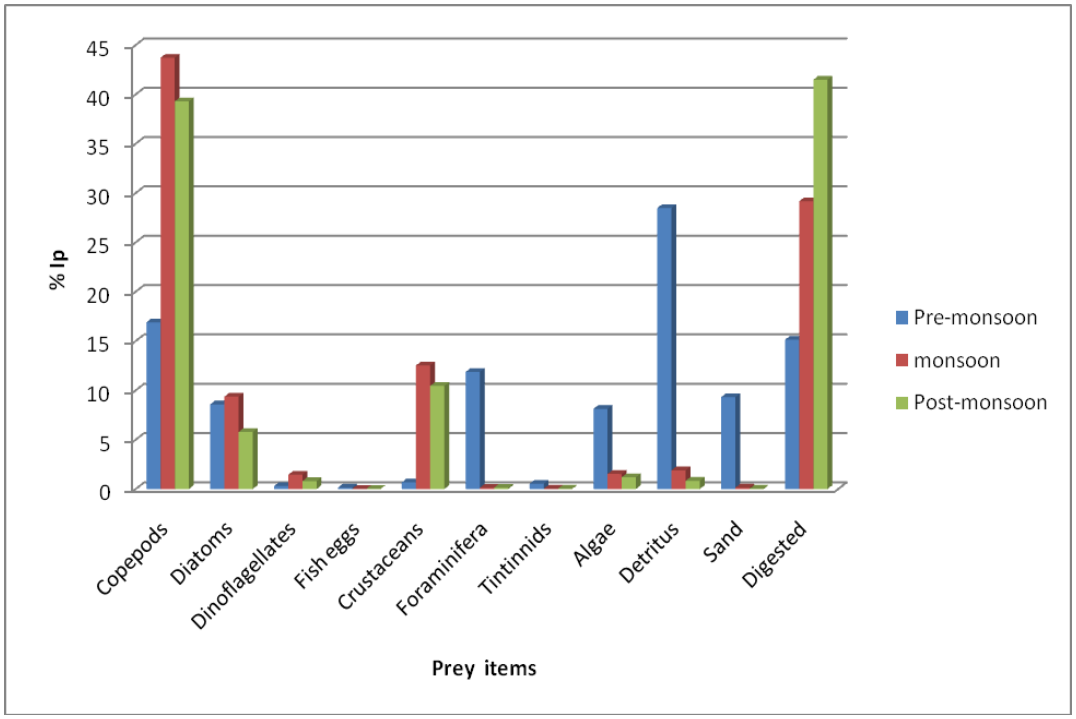


Fig. 3.4. Seasonal percentage Preponderance Index (% Ip) showing dominance of various food items

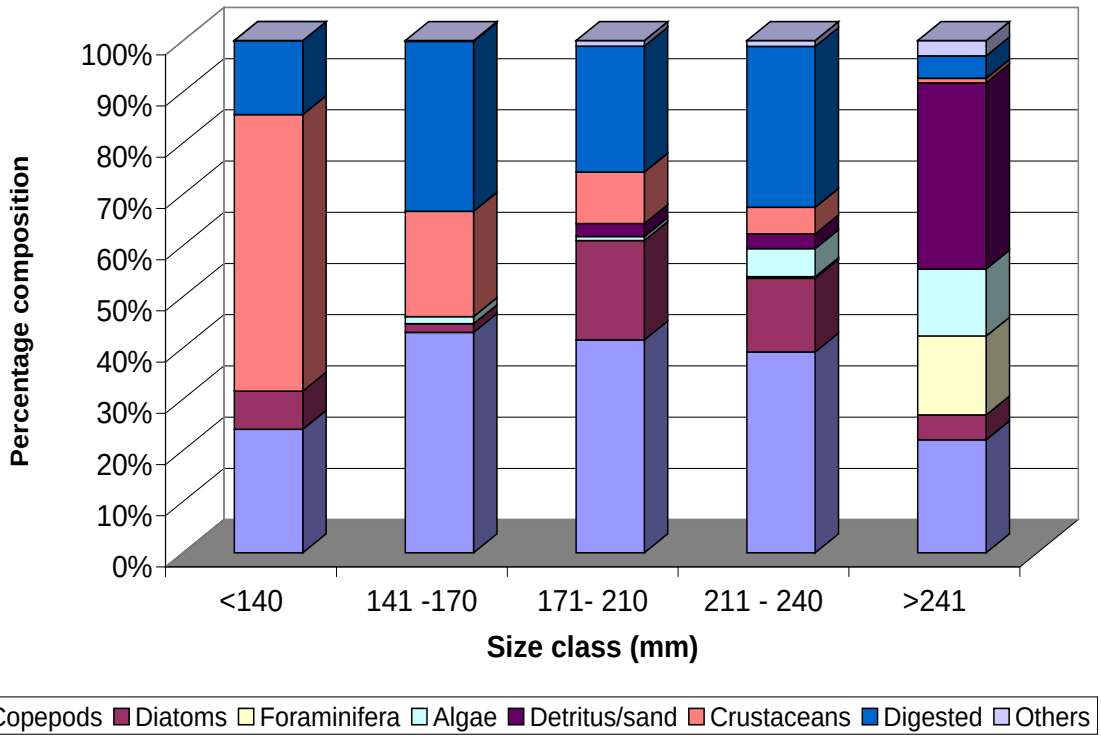


Fig. 3.5. Percentage composition of diet items in the various size groups of Indian mackerel

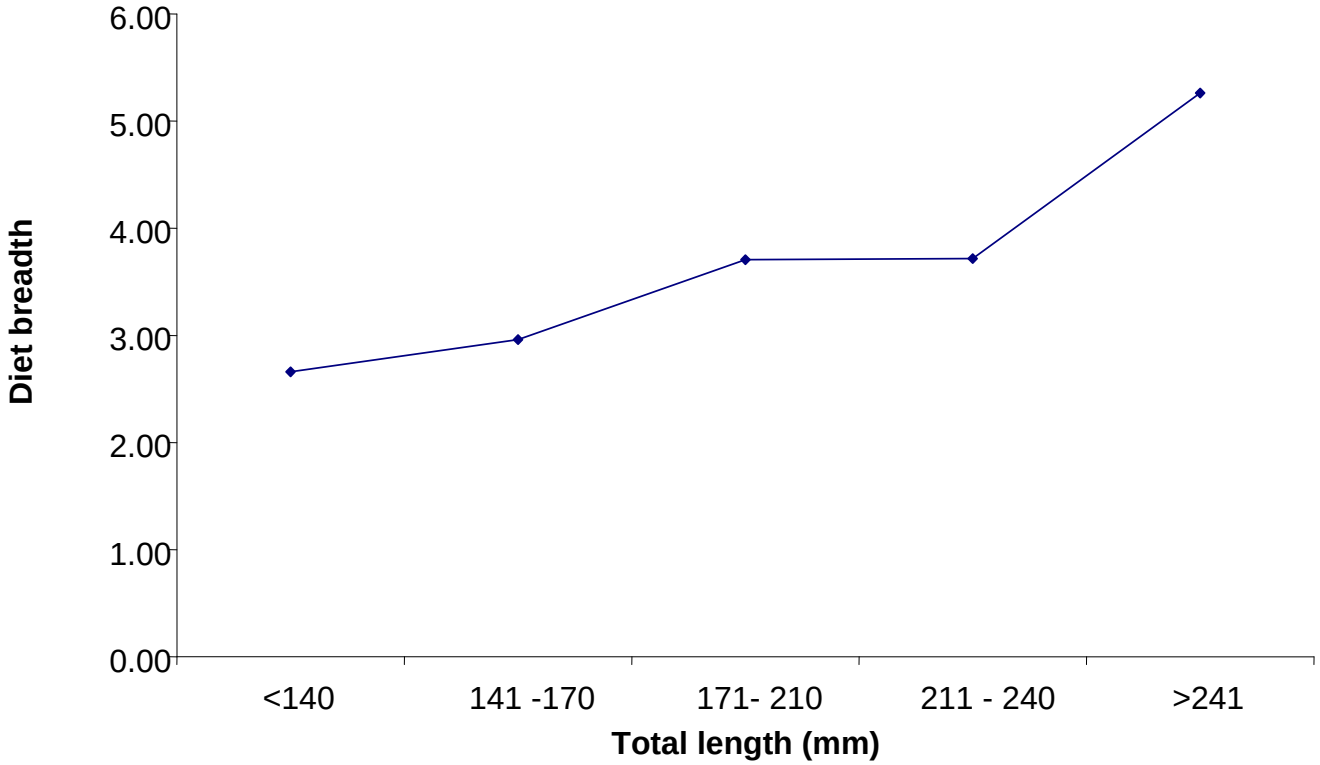


Fig. 3.6 Diet breadth (B) among various size groups of mackerel

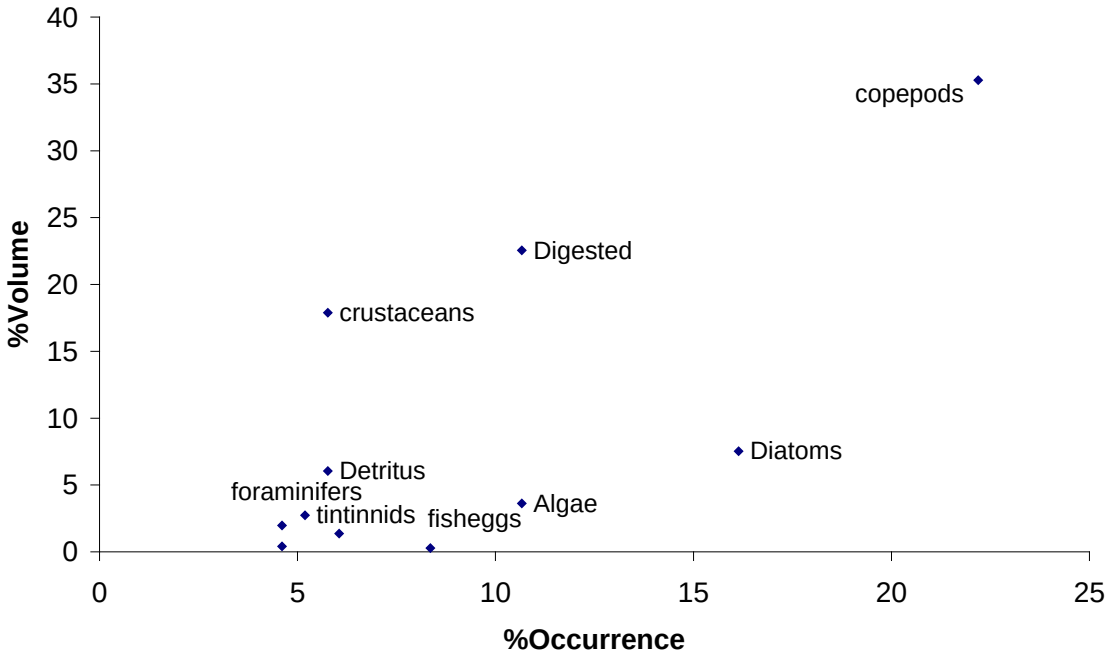


Fig. 3.7. Costello analysis indicating the occurrence and dominance of different prey items

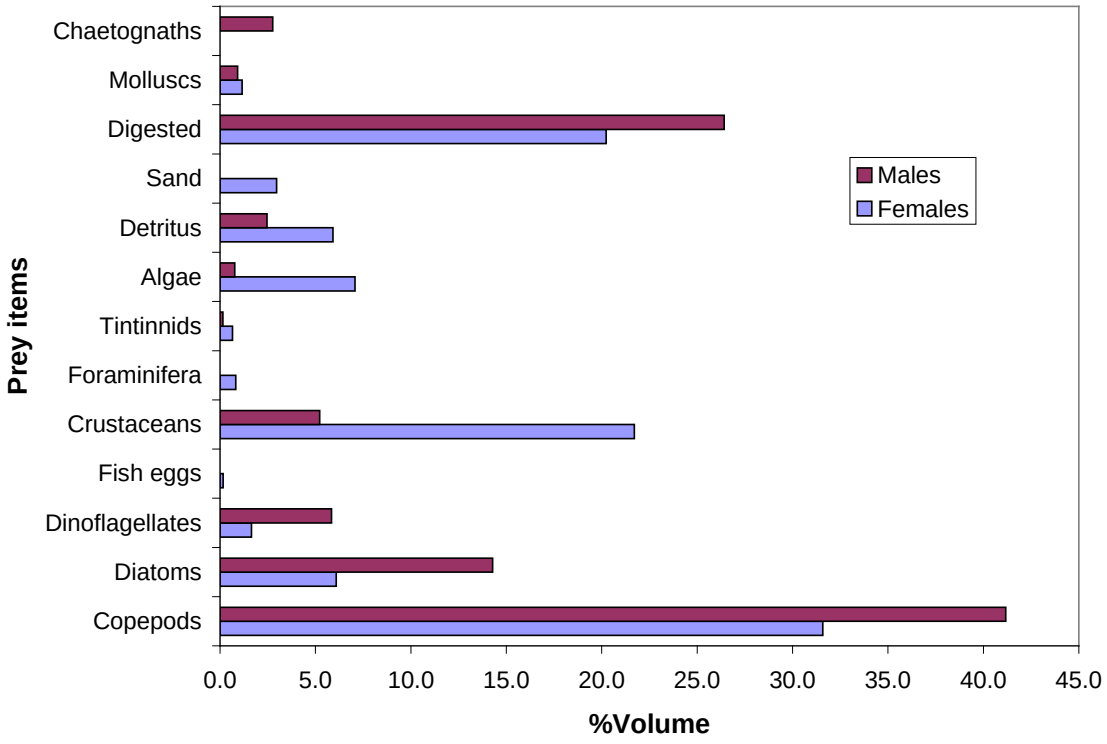


Fig. 3.8. Volumetric indices of various food items among sexes in *R .kanagurta*.

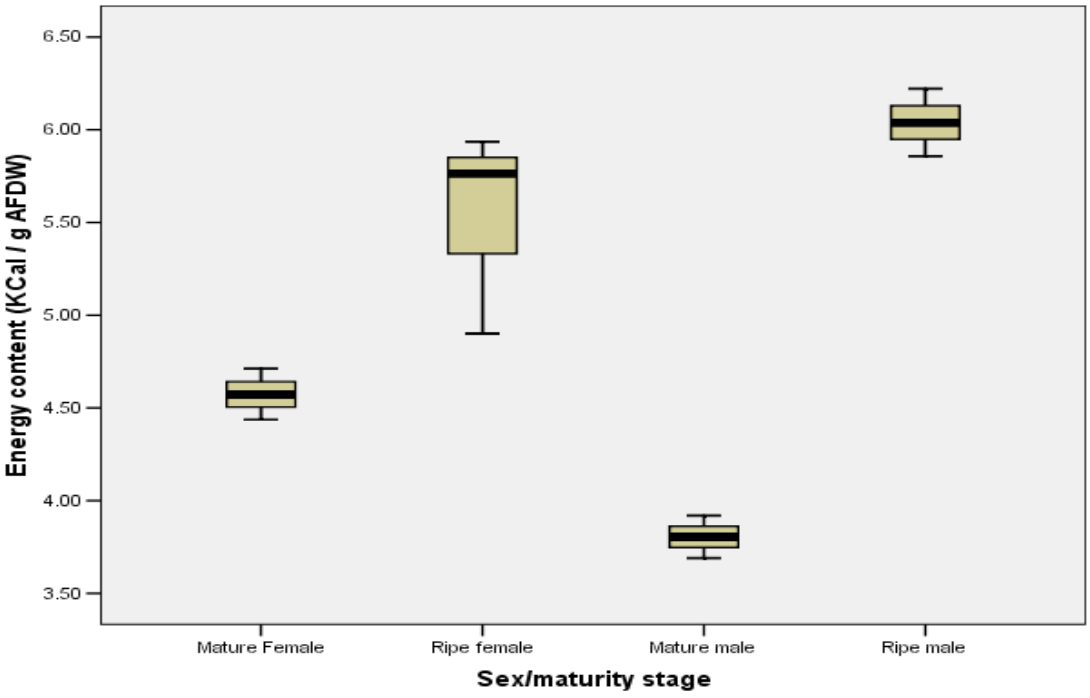
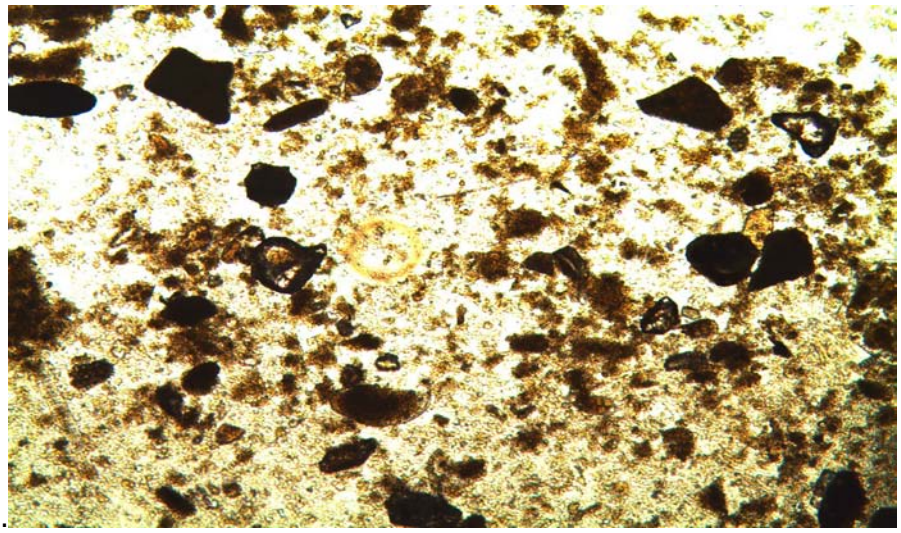
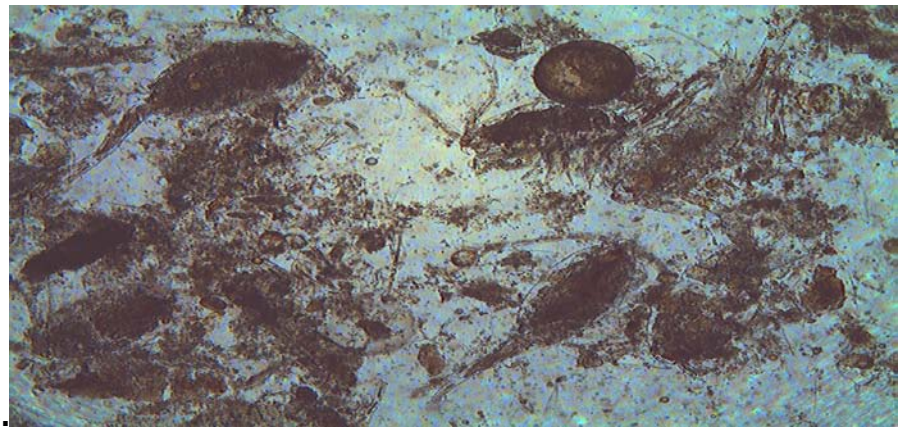


Fig.3.9. Box plot indicating the variations in energy content in muscle tissue of different sex and maturity stages of mackerel

A. 

B. 

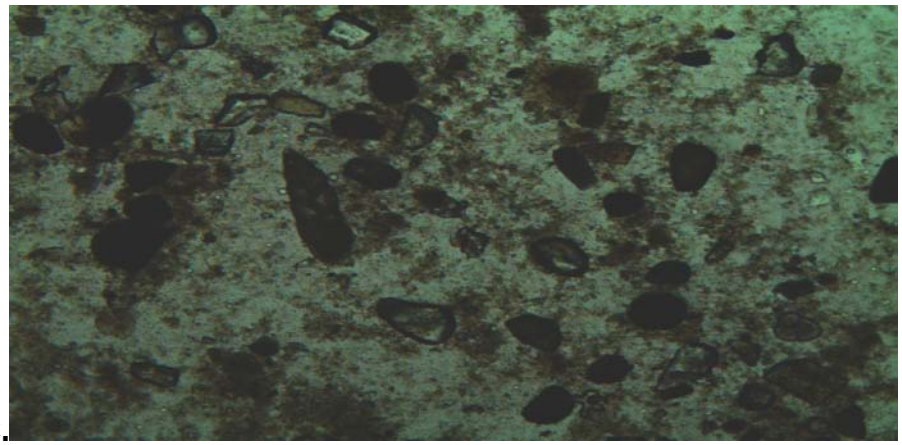
C. 

Plate 4.Snapshots of mackerel diet indicating dominance of: (A) phytoplankton, (B) copepods and (C) detritus

3. 5. Discussion

3.5.1. Feeding Intensity: It is reported that fish metabolism has an influence on feeding behavior and feed intake by fish is such that it meets their energy requirements (Bowen *et al*., 1995). Thus if a diet has low energy value, fish will compensate by eating more within the limits of its stomach capacity (Mittelbach, 2002). Therefore, this may be one reason why during the pre-monsoon season when the low energy value food constituted by detritus was predominant, the occurrence of stomachs with moderate to active feeding activity was the highest.

The rapid increase in the feeding intensity in the 171 – 230 mm size group and progressively thereafter was coinciding with the length at which maturation is initiated and spawning activities predominate in this species (Yohannan, 1979, 1995; present study Chapter 2). Typically, when fishes approach maturity they are found to increase the energy devoted to gonad development by increased feeding intensity (Iles ,1974; Lambert and Dutil, 1998) which supports the observations in this study.

Although intensity of feeding in mackerel has been reported to vary with maturity and spawning conditions, being minimal during spawning, high in the maturing group, and maximum during post-spawning period (Bhimachar and George, 1952; Chidambaram *et al*., 1952; Noble, 1962; Rao, 1965) no such decline in feeding activity of maturing or ripe fishes was observed in the present study. This agrees with the observations recorded by Kuthalingam (1956) and Krishnamoorthi (1971) in the Indian mackerel and threadfin bream respectively. The observation that egg production in many fishes depends more on the energy

intake during the spawning season than on the energy reserves accumulated earlier (Dominguez-Petit and Saborido-Rey, 2009) and increased feeding during maturation which enables development of gonadal growth without slowing of somatic growth (Milton *et al.,* 1994) supports the observation of intensive feeding by ripe spawners in Indian mackerel. Feeding intensity declined in the largest size groups (>231 mm) probably in tune with the reported slowing down of growth as it reaches its asymptotic age/length (Yohannan, 1979) which is a common phenomenon in all fishes.

3.5.2. Diet composition

3.5.2.1. Diet composition in relation to seasons: The ranking of various food items based on the Index of Preponderance (I_p) indicated seasonal variations in diet composition with detritus ranked first followed by copepods during the pre-monsoon season. Copepods, 'digested matter' complex and crustaceans dominated during the monsoon and post-monsoon period (Table 3.3). This observation agrees with the findings of Schaefer *et al.* (2002) and Kulbicki *et al.* (2005) that many fishes are opportunistic feeders eating what is available within a more or less restricted range of items and changes in number of prey types reflect only this plasticity as well as the variability of prey in the particular biotope where the fish is feeding. The dominance of detritus during the pre-monsoon is probably a habitat-shift associated diet change and indicative of bottom feeding habits (Kutty, 1965) that occurs during its "demersal phase" coinciding with the declining of thermocline during the pre-monsoon period (Murty and Vishnudatta, 1976; Yohannnan and Abdurahiman, 1998). Opportunistic demersal feeding has

also been noted in several other scombroids such as tunas (Manooch *et al*., 1985; Griffiths *et al*., 2007). The observations are supported by several reports which indicate that digestion of detritus can supply the consumer with energy and therefore detrital aggregates which are not a normally acceptable food resource may serve as a short-term food resource if the consumer can tolerate a temporary nutritional deficiency (Peters and Kjelson, 1975; Bowen, 1979; Peters and Schaff, 1981; Ahlgren, 1996) which may be applicable in the Indian mackerel also.

3.5.2.2. Diet composition in relation to size groups: In the present study the feeding habits of the different size groups indicated differences in their prey preferences agreeing with the observations made by some earlier workers (Chidambaram, 1944; Rao and Rao, 1957; Rao, 1962). The ontogenetic diet variations indicated in the present study are also supported by the observations of Kapoor *et al*. (1975) that the length of the alimentary canal is indicative of the food preferences of the fishes with carnivores having the smallest gut length and detritivores the highest and that by Rao and Rao (1957) who observed differences in the relative length of the alimentary tract of juvenile and adult mackerel and attributed it to differences in their feeding habits. The occurrence of macroalgae in relatively large sized bottom feeding specimens during the pre-monsoon was observed. This observation is supported by the fact that larger fish have the capability to digest even low-quality food and therefore often meet their energetic demands by consuming macroalgae (Benavides *et al.,* 1994).

Ontogenetic changes in foraging patterns are linked to prey profitability and have consequences for the growth process of the fish (Galarowicz *et al.,* 2006). There is tendency for fish size to increase with depth (MacPherson and Duarte, 1991) and in the case of the Indian mackerel which migrates to deeper waters, diet shifts are probably tuned for utilization of energy from all possible sources. Thus, Diet breadth (B), as an indicator of diet diversity was highest in the size class > 230 mm indicating that the larger individuals are capable of exploiting a broader range of prey and have more generalized feeding habits compared to < 140 mm size groups. According to Mohamed *et al.* (2005) ontogenetic shifts in trophic levels of animals must be considered in mass-balance ecosystem modeling studies. This study was confined to the Indian mackerel which is the second largest marine fishery resource contributing to the annual fish catches of the Kerala state. Very few reports of ontogenetic diet shifts, if any, are available for marine fishes in Indian waters and this study indicates that it may have to be assessed for other species as well to understand the energy flow of the marine ecosystem off Kerala coast and make meaningful fishery projections through trophic modelling.

3.5.2.3. Diet composition and energy variations: Observation of copepods as an important food item irrespective of seasons or size in the Indian mackerel agrees with earlier studies (Bhimachar and George, 1952; Noble, 1962; Pradhan,1956; Rao and Rao,1957; Sivadas and Bhaskaran, 2008). Prokopchuk and Sentyabov (2006) also have reported that calanoid copepods are the favored food items of mackerel. Prey availability is the key factor in determining feeding

behavior in fishes (Dorner *et al*., 2003) and the diet composition of fishes is often related to temporal fluctuation in the zooplankton assemblage in the environment (Mostardo *et al.,* 2007) or availability of other prey fishes (Persson and Bronmark, 2002; Galarowicz *et al.,* 2006). Thus the preference to copepods by all size groups indicated in the present study may be due to availability as they are the most abundant item in the zooplankton of the Arabian Sea along the southwest coast of India (Raymont, 1983; Gopinathan *et al*., 1984; Madhupratap, 1999; Mohamed *et al*., 2006; Smith and Madhupratap, 2005). Besides, the preference for copepods can be justified because invertebrate prey is reported to provide the highest food quality in terms of both protein and energy compared to the primary food resources of algae, macrophytes and detritus (Qasim *et al*.,1973; Bowen *et al.,*1995). Selective predation on copepods and crustaceans, by maturing fish which enables them to continue to grow rapidly while developing gonads has been reported (Milton *et al.,* 1994) which is another reason it might be a preferred food item. Hunter and Leong (1981) reported that anchovy *Engraulis mordax* required a daily ration of copepods equivalent to 4-5% of female wet weight per day to support the annual cost of growth and reproduction. Therefore it may be concluded that copepods abundant in the Arabian Sea ecosystem are an important link in the energy transfer to fishes, especially mackerel, an important fishery resource of the region.

The Indian mackerel is classified as predominantly plankton feeder but detritus was observed to be the most important diet item during the pre-monsoon period coinciding with its peak spawning period. Several studies have suggested

that organic detritus which consists of all types of biogenic material in various stages of decomposition and settled detritus (chitinous material, plant fibres, phytoplankton cell remains, remanants of exoskeleton of zooplankton, sponge spicules, stems of hydrozoans, foraminiferans, broken shells of clams, gastropods, fish scales/bones and large quantities of silt, sand and clay along with micro and meiobenthos) are a significant resource for those consumer organisms which are capable of exploiting bacterio-organic complexes in the water (Rajan, 1968; Qasim, 1972; Jacob and Rajagopal, 1980; Newell, 1984; Wilson, 2002). Rajan (1968) who studied the food spectrum of fishes from the Chilka lake found even some well known carnivorous fishes to feed on detritus even while other food organisms were readily available. The seasonal dominance of detritus in the diet observed agrees with the observations by Mann (1988) that although fresh algal sources are a superior source of energy compared to detrital particles, the fact that phytoplankton production is seasonal while detrital particles are available around the year makes it a supplementary food source during the periods of low algal abundance. In the Cochin backwaters, peak phytoplankton production occurs mostly during monsoon and post-monsoon season caused by monsoon induced upwelling and winter cooling effects as compared to pre-monsoon season which has very low primary production (Gopinathan *et al*., 1984; Madhupratap *et al*., 2001) while detritus is reported to be maximum during the April –June period with its nutritive value in terms of C : N ratio ranging from 5 - 10.5: 1 (Qasim and Sankaranarayanan, 1972).

Galloop *et al.* (1999) has reported that detrital material is a source of monounsatured (C14: 1 – C18:1) fatty acids (MUFAs) as well as saturated fatty acids (SFA) such as C20:0. The major source of energy in fishes are monoenes and saturates among fatty acids and selective ingestion of detritus by fish has also been reported (Ahlgren, 1996). Therefore it is quite possible that detritus is being ingested purposefully by mackerel depending on the exigencies of the environment. Wilson (2002) had indicated that because of an increase in microbial activity during the summer season due to elevated temperatures there is an increase in protein levels of detritus during this period. Incidentally the summer or pre-monsoon period was the period when increased detritus consumption was observed in mackerel indicating the importance of detritus in the diet of mackerel. Madhupratap *et al*. (1994) hypothesized the importance of detritus food chain in determining the success of mackerel fisheries *vis-à-vis* oil sardine during periods of adverse environmental conditions resulting in less than optimum plankton production. However, detritus is seldom mentioned in earlier diet composition studies of mackerel except as an incidental food item (Vivekanandan *et al*., 2009) and it thus appears that the role of detritus as a feed component has not been properly evaluated for Indian mackerel. Studies by Madhupratap *et al.* (1994) have indicated that the microbial loop may be a significant factor in ensuring energy supply in the marine food web, which is reiterated in this study. Therefore a more detailed evaluation from different regions/ecosystems along the coast may be rewarding to understand the dynamics of energy transfer in the marine food web.

Because of its varied diet that includes plant and animal matter the Indian mackerel may be considered as an omnivore. Omnivory is a feeding strategy that enables fish to complement protein from invertebrate prey like copepods with energy from the more abundant primary foods such as detritus and algae, especially when their favored food items are scarce (Bowen *et al*., 1995). No differences in the energy levels among the sexes was observed in the study indicating it as an opportunistic feeder where diet broadly reflects availability and habitat characteristics. However the higher energy levels observed in ripe stages compared to mature stages in both sexes is probably due to the intensity of feeding being higher as maturity progresses.

The present study was confined to studying the food items available in the guts at the time of analysis which revealed that there are seasonal variations in diet and physiological factor like maturation are also influencing feeding patterns. However a time–integrated diet picture is not available for any species including mackerel in Indian waters, and may be gainfully by employing more advanced techniques such as stable isotope studies there will be a more clear elucidation of the energy flow in this ecosystem which will also facilitate an understanding of the factors influencing the annual variations in the fishery.

****

CHAPTER 4
LIPID DYNAMICS

CHAPTER 4

LIPID DYNAMICS

4.1. Introduction

Lipids and specifically their constituent fatty acids play an important role in the life histories and physiology of fishes as they are an important source of energy for their growth, reproduction and movement, including migration (Sargent, 1989). Lipids in fishes are typically constituted by triacyl glycerols which are an energy reserve, and phospholipids which are more important as part of cellular structure. Fatty fishes (> 2% lipid) such as mackerel, sardines and herring store fat in their muscle mostly as triglycerides while lean fishes such as cod and haddock are reported to store fat in their livers (Ackman, 1980). As lipids and their constituent fatty acids play a crucial role in ensuring reproductive success, enhanced larval survival and growth have been studied in detail for many species of aquaculture importance to develop improved diets especially in their early stages (Bromage and Roberts, 1995; Sargent *et al*., 2002; Tocher, 2010). However, only few studies have been conducted in species which are mostly caught from the wild but are yet of commercial importance. Tocher (2003) comments that molecular technologies are being applied in the area of fish lipid metabolism presently for aquaculture purposes such as increased production or value-addition of nutrient (EPA and DHA) composition of fish for balanced diets but ultimately they may also be used for assisting efforts to understand and possibly reverse the ongoing decline in wild fish populations.

The biochemical composition of Indian mackerel with regard to food processing technologies has been reported earlier but few studies relating it to its biological cycles such as feeding, growth and reproduction which could possibly improve the understanding of the dynamics of the resource have been made. Lipids play an important role in the life-history dynamics of fishes, especially regarding reproduction and are mostly sourced from their natural diet. Hence this study focused on the fatty acid profile of mackerel in relation to its maturity stage, spawning cycle and feeding habits.

4.2. Review of Literature

4.2.1. Role of lipids and fatty acids in fish: The major role of lipids in fish is for the storage and provision of metabolic energy in the form of ATP provided through ß oxidation of fatty acids (Sargent *et al*., 2002). Lipids can be broadly divided into two groups- polar lipids composed principally of phospholipids and neutral lipids composed principally of triacylglycerols (Tocher, 2003) and are stored in muscle, skin or liver in fishes. Ratnayake and Ackman (1979) reported that skin and muscle are the most important fat storage organs in mackerel compared to other species where it is stored in the liver (capelin); and muscle tissue (herrings). Lipid mobilization is reported to be very active in fish during the period of gonad growth and maturation (Henderson and Wong, 1998). While in females the mobilization increases the gonad weight and deposition of fat in certain parts of the body, in males it is more associated with behavioural aspects of reproduction including development of secondary sexual characters and enhanced swimming activity (Henderson *et al*., 1984). Lipids are composed of fatty acids that are

designated on the basis of their chain lengths, degree of unsaturation and the position of ethylenic bonds into 3 major groups, namely, saturated fatty acids (SFAs), monounsaturated fatty acids (MUFAs) and polyunsaturated fatty acids (PUFAs) (Ackman, 1982).

Fatty acids (FA) have three major role in fishes, namely, i) as fuels, ii.) as membrane components and iii.) as precursors of eicosanoids that produce prostaglandins which have a critical role in mediating reproductive activities (Bell *et al*., 1986). Thus, FA play a critical role in the maturation and reproductive success, hatching and enhanced larval survival as well as growth patterns and hence have been used to understand maturation, spawning and recruitment dynamics of many finfish and shellfish species worldwide (Appa Rao, 1967; Rao, 1967; Nikolskii, 1969; Henderson *et al*., 1984; MacFarlane *et al*., 1992; Ballantyne *et al.*, 1996; Bell and Sargent, 1996; Jong *et al*., 1997; Galap *et al*., 1999; Kas'yanov *et al.*, 2002; Mourente *et al.*, 2002).

SFAs function as important oxidative substrates for a variety of tissues including red muscles whose activity is high during spawning migrations (Shulman and Love, 1999). The ratio of PUFAs like docosahexaenoic acid (DHA, 22:6n3), eicosapentaenoic acid (EPA, 20: 5n3) and arachidonic acid (AA, 20:4n6) are critical for normal growth and reproduction in fishes (Furuita *et al*., 1996; Sargent *et al*., 1999, 2002). Stacey and Goetz (1982) and Henderson *et al.* (1985) reported conversion of PUFAs to prostaglandins which are essential for ovulation in all vertebrates including fish (Murdoch *et al.,* 1993). Certain fishes are reported to use prostaglandins to synchronize spawning behaviour between sexes (Bell *et al*.,

1986). Certain lipid classes such as phospholipids are important constituents of fish egg yolk and selective utilization of monoenoic and polyenoic fatty acids has been reported during process of yolk deposition and oocyte maturation in fishes (Henderson *et al*., 1984, 1984a; Wiegand and Idler, 1985; Navas *et al*., 1997; Sorbera *et al.,* 2001; Johnson, 2009). Mckenzie *et al*. (1998) noted maximal swimming speed of salmon positively correlated with muscle levels of C18 FA and suggested that monoenoic FA rather than PUFA are preferred fuels in swimming muscles.

It is now sufficiently established that fatty acid compositions of the neutral lipids in animal depot fat are dictated by the products of the animal's metabolic activity as well as the fatty acid components of its dietary lipids (Ackman, 1980). In most marine species of fish, natural diets are a good source of fatty acids (Tocher, 2003) and Ackman *et al*. (1980) reports that in many marine fishes, fatty acid biosynthesis essentially follows the chain elongation route C16:0 ➔ C18:0 ➔ 18:1n9 when food supply is adequate and additional unsaturated acids are not required. However, fishes lack the Δ12 and Δ15 (n3) desaturase enzymes and hence cannot form 18:2n6 and 18:3n3 fatty acids from 18:1n9 thereby making these FA essential fatty acids that have to be provided through the diet which will be desaturated further and elongated to form the physiologically essential C20 and C22 PUFAs (Tocher, 2003). Thus, fishes acquire PUFAs in two ways- a) through the food chain and b) synthesis of long chain FA from shorter carbon chains through enzymes known as desaturases and elongases (Shulman and Love, 1999). In fishes, besides the significant contribution of PUFAs from dietary

sources, monoenes and saturated fatty acids are also synthesized *de novo* (Watanabe, 1982; Shulman and Love, 1999). The essential fatty acid (EFA) requirements of fishes have been extensively studied and known to vary qualitatively and quantitatively (Sargent *et al*., 1995; Bell and Sargent, 2003).

4.2.2. Fatty acid composition in fishes: The specificity of fatty acid oxidation regulated by enzyme systems is the critical factor determining the species level fatty acid composition of fishes (Tocher, 2003). Nordgarden *et al*. (2003) attributed the seasonally changing fatty acid composition in fishes due to metabolic changes in the ß oxidation capacity. The polyunsaturated fatty acids (PUFAs) of the n3 family associated with fish and fish oils are shown to have beneficial effects on prevention of heart diseases in humans and hence many studies have addressed the total lipid and fatty acid composition of fish which have revealed profound variation among species (Exler *et al*., 1975; Exler and Weihrauch, 1976; Gooch *et al*., 1987; Kryznowek and Murphy, 1987; Kryznowek *et al*., 1989; Gopakumar, 1993). Many species have been studied for fatty acid variations in relation to seasons, size groups or maturity and it has been observed that fatty acid composition of fish differs due to climatic conditions, diet, age, maturation and also among various species (Knipparath and Mead, 1966; Gopakumar, 1969; Culkin and Morris, 1970; Hardy and Keay, 1972; Toyamizu *et al*., 1976; Ueda, 1976; Hayashi and Takagi, 1977, 1978; Kinsella *et al.,* 1977; Nair and Gopakumar, 1978; Ota *et al*., 1980; Linko *et al*., 1985; Clarke and Holmes, 1986; Nichols *et al.,* 1986; Gallagher *et al*., 1984, 1989; Vlieg and Body, 1988; Henderson and Almatar, 1989; Kharlamenko *et al.,* 1995; Schwalane *et al*., 1993; Belling *et al.,* 1997, 2001; De

Silva *et al*., 1997; Gunasekera *et al*., 1999; Saito *et al.,* 1999; Bandarra *et al*., 2001; Budge *et al*., 2002; Lea *et al*., 2002; Osako *et al*., 2003; Robin *et al*., 2003; Halilogulu *et al.,* 2004; Rosa *et al*., 2004, 2005; Velansky and Kostetsky, 2008). Gruger *et al*. (1964) reported the fatty acid composition of oils from 21 species of marine fish, fresh water fish and shell fish. Nair and Gopakumar (1978) reported on fatty acid composition of fifteen species from Indian waters while Osman *et al.*(2007) reported on lipid content and fatty acid composition of thirteen marine fish species of Malaysia including the Indian mackerel. Yamada and Hayashi (1975) reported the FA composition of 22 species of finfish and molluscs from the Japanese seas. Turan *et al*. (2007) reported on the fatty acid profile of the thornback ray *Raja clavata*. Saito *et al*. (1997) reported on the differences in the FA composition of bonito tuna in tropical and temperate localities. Hazra *et al*. (1998) reported seasonal variation in lipid and FA composition of 3 species of puffer-fishes from Indian waters while Saito *et al*. (1999) investigated influence of diet on FA composition of certain caesionid and siganid fishes. Wiegand (1996) reports that in fishes there is selection pressure to maintain levels of DHA in eggs within a species-specific range. The physiological selective accumulation of DHA in muscle tissues of active fishes such as mackerel and tunas (Saito *et al*., 1995; Osako *et al*., 2006) and low DHA content (<20% of total lipids) in several non-migratory fishes such as *Solea solea* (Goekce *et al*., 2004) and *Pagrus major*, *Lateolabrax japonicus*, *Seriola dumerili*, *Paralichthys olivaceous* and *Caranx delicatissimus* (Aoki *et al*., 1991) are reported. High levels of AA (7.4 – 14.9%) in muscle lipids of

several species of marine fishes of Australia (Dunstan *et al*., 1988) has also been reported.

4.2.3. Lipids and maturation dynamics: Lipid mobilization is reported to be very active in fish during the period of gonad growth and maturation (Nikolskii, 1969; Mourente *et al*., 2002). While the mobilization increases the gonad weight in females and deposition of fat in certain parts of the body, in males, it is more associated with behavioural aspects of reproduction including development of secondary sexual characters and enhanced swimming activity (Henderson *et al.,* 1984; Ballantyne *et al*., 1996). Marshall *et al*. (1999) investigated usage of lipid energy as a proxy for total egg production by fish stocks. Jong *et al.* (1997) studied lipid accumulation and fatty acid composition during the maturation process of three pelagic fishes belonging to family Comephoridae in Lake Baikal. Gallagher *et al*. (1989) reported that in the striped bass *Morone saxitilis* fatty acid composition varied significantly in relation to size. Gopakumar (1969) observed that there was a rapid increase in the lipid content in muscle of oil sardine *Sardinella longiceps* during the months preceding maturation of the ovaries and a sharp decline after spawning. Chidambaram *et al.* (1952) reported that mackerel along the Calicut coast are fatty during March - May and while the fat in muscle tissue of immature mackerel was always below 3%, in mature ones it is was as high as 8.5% with fish becoming lean after spawning.

Changes in lipid content and its fatty acid composition during the sexual maturation and spawning process in capelin, *Mallotus villosus* (Henderson *et al.,* 1984) and northern bluefin tuna *Thunnus thynnus* (Mourente *et al*., 2002) were

reported. Environmental temperature is another important factor determining fatty acid composition in fishes (Farkas *et al*., 2001) and the combined effect of environmental temperature and diet on formation and deposition of fatty acids in carps has been reported by Farkas *et al*. (1980). Lasker and Theilacker (1962) described the FA composition of lipids of tissues of Pacific sardine in relation to ovarian maturation and diet. Rosa *et al*. (2004, 2005) studied changes in the lipid profile of the cephalopods such as *Illex coindetii* and *Todaropsis eblanae* (ommastrephid squids) as well as *Octopus vulgaris* and *O. delfilippi* (octopus) in relation to sexual maturation. Ballantyne *et al.* (1996) who investigated sex-specific changes in plasma non-esterified FA of sock eye salmon (*Oncorhynchus nerka*) during their spawning migration found sex related differences in the proportion of four fatty acids namely 16:0, 18:1, 20:5 n 3 and 22:6n3 while n:6 series of FA were significantly higher in males than females. Henderson *et al*. (1984) demonstrated increased utilization of MUFA in the muscles of the male capelin *Mallotus villosus* associated with enhanced physical activity and migration for spawning as compared to females. Cejas *et al.* (2003) reported lipid and FA composition of ovaries from wild fish and eggs from captive fish of white sea bream *Diplodus sargus*. According to Tocher (2003) eicosanoid production which is critical in influencing reproductive activities in fishes is influenced by the cellular ratio of arachidonic acid (AA, C20:4n6) and docosahexaenoic acid (DHA, C20:5n3). The ratio of the fatty acids DHA: EPA: AA is found to be critical in determining egg quality of fishes (Bruce *et al.*, 1999; Bell and Sargent, 2003). Varljen *et al*. (2004) related seasonal variation in AA levels of *Diplodus vulgaris* to the process of active

vitellogenesis occurring during summer. Ballantyne *et al.* (1996) found increased levels of AA which was higher among males in the plasma of salmon mobilized from muscle reserves for spawning migration. Kozlova and Khotimchenko (1993) noted that DHA content in liver tissue of several species of fishes of Lake Baikal decreased during spawning presumably being mobilized for egg production.

4.2.4. Fatty acids in relation to feeding dynamics: In spite of diet and environment induced variations in fatty acid profiles among individual fishes, the fatty acid signatures of each species is unique and this has been effectively used to understand their foraging ecology and marine food web dynamics (Kirsch *et al*., 1998; Iverson *et al.,* 1997, 2002; Turner and Rooker, 2005; Recks and Seaborn, 2008). It is reported that microscopic algae produce a number of fatty acids that animals are incapable of synthesizing and these are usually conserved when passed through the food web (Ackman, 1980; Cripps *et al.,* 1999). Gatten *et al*. (1983) observed that during larval development in herrings the saturated fatty acid (SFA) component remained constant whereas the polyunsaturated fatty acids (PUFA) and monosaturated fatty acids (MUFA) components changed, progressively favoring the latter group which was in tune with a shift in their feeding preferences for calanoid copepods from algae. Predominance of 16:1n7 FA in diatoms (Ackman *et al.,* 1968) and bacteria (Wilkinson, 1988) has been reported. According to Anderson and Pond (2000) diatoms contain relatively higher levels of EPA (20:5n3) compared to DHA (22:6n3) while the converse is true in dinoflagellates which are richer in DHA. Ackman *et al*. (1981) observed that wax esters from a diet of copepods are potentially the major sources of docosenoic

acids in fish. While most marine fishes acquire DHA, EPA and other HUFA which are critical to their growth and survival through the marine food chain, some are also reported to be capable of acquiring it through symbiotic bacteria that live in their intestine (Yano *et al*., 1994; Yazawa, 1996) and such inter-specific differences in DHA acquisition routes have been hypothesized to contribute to population changes among pelagic fish species (Masuda, 2003). FA profiles of apex predators such as sharks, sea-birds and seals have been used to match it with the most likely combinations of prey FA signatures (Iverson *et al*., 1997; Raclot *et al.,* 1998). Mayzaud *et al*. (1999) recommended caution while considering use of fatty acid markers in omnivorous species where there is simultaneous ingestion of phytoplankton and zooplankton. Phillips *et al.* (2003) used a combination of stomach contents data and fatty acid composition of various tissues of Southern Ocean squid *Moroteuthis ingens* to study the ecological variations in its diet. Kharlamenko *et al.* (1995) used fatty acid ratios such as sum of branched FA, concentration of 18:1n7, 20:5n3 and 22:6n3 FAs and the sum of C18 and C20 PUFAs to understand food web dynamics. Interspecies differences in fatty acid composition of myctophids have been related to dietary differences (Saito and Murata, 1998; Lea *et al*., 2002). Bishop *et al.* (1976) related lipid composition of slender tuna as related to their food. Recks and Seaborn (2008) reported exclusive levels of short chain saturated fatty acids such as C14:0 and C15:0 related to its omnivorous diet including microalgae, macrophytic detritus and inorganic sediments rich in absorbed microorganisms. However few studies on the

above aspects are available for the multitude of commercially important fishes from the Indian waters.

4.2.5. Lipids and fatty acid composition of Indian mackerel: The Indian mackerel *Rastrelliger kanagurta* is an important food fish in India and an important forage item for top predators such as tunas in the marine food web. Based on the lipid composition mackerel can be classified as a medium fatty fish whose mean fat content is about 3.29% and varies between 0.97 – 6.3% (Venkataraman and Chari, 1951; Gopakumar and Nair, 1971; Mathew *et al*., 1999; Osman *et al*., 2001, 2007). Venkataraman and Chari (1951) noted fat variations in mackerel had a strong relationship with feed availability (plankton) and more variations in fat content among the individuals belonging to larger size groups. Chidambaram *et al*. (1952) studied fat variation in Indian mackerel in relation to biological parameters such as size, seasons, food/feeding and spawning. Seasonal variation in fat content the Indian mackerel reportedly occurs with highest levels during October to November and March to May period along the Calicut coast coinciding with its spawning peak (Devanesan and John, 1940; Chidambaram *et al*.,1952; Venkataraman and Chari, 1953). However no information is available on the variations in the fatty acids constituting the lipids in relation to biological processes.

The biochemical composition of Indian mackerel with regard to food processing technologies has been reported earlier (Gopakumar and Nair, 1971; Nair *et al*., 1976; Nair and Gopakumar, 1978, 1984; Mukundan *et al*., 1981). The compilation of biochemical composition of major Indian food fish and shellfish from marine, brackish water and fresh water (Gopakumar, 1993) refers to, among

various fishes, the total lipid content of mackerel but does not mention its fatty acid composition. Osman *et al*. (2001, 2007) reported lipid and fatty acid composition of Indian mackerel *R. kanagurta* found in Malaysian waters.

4.3. Materials and Methods

4.3.1. Fish sampling: Fresh mackerel caught in ring seines and trawls operated off Cochin and landed at Cochin Fisheries Harbour in the months of January and May 2007, representing the post-monsoon and pre-monsoon seasons respectively were used in the study. The freshly caught specimens were transported using ice to the laboratory where the following parameters were recorded for the individual fishes: total length (mm), weight (g), sex and gonad weight (g). A random selection of mackerel of both sex classified into immature and mature stages based on the appearance of the gonads as given below was used,

Immature: Gonads not fully developed, small in size being less than half of the body cavity. Ovary pinkish and tubular, most advanced oocyte diameter < .15 mm; Testes small whitish and leaf-like.

Mature: Gonads well developed. In females, ovaries are bright yellow to orange-red colour, blood vessels well developed and opaque/transparent ova with ova diameter range >0.5mm; in males testes whitish and occupying more than half body cavity.

4.3.2. Muscle tissue sample preparation: Fishes were grouped according to sex and maturity stage for the study and muscle tissue (with skin) weighing about 30 g from each fish cut from just below the first dorsal fin was used for the extraction of lipids and preparation of methyl esters (Table 4.1).

Table.4.1. Biological details of mackerel selected for fatty acid profiling

Sampled month	Mean TL (mm) /weight (g)	Male Immature	Female Immature	Male Mature	Female Mature
January	TL	178 ± 12	184 ± 11	197 ± 5	205 ± 12
	Weight (g)	63 ± 5	79 ± 14	105 ± 9	155 ± 16
May	TL	179 ± 22	171 ± 27	220 ± 15	242 ± 25
	Weight (g)	72 ± 6	76 ± 8	167 ± 8	190 ± 14

4.3.3. Lipid extraction and preparation of methyl esters: Samples of muscle tissue (including skin) cut from below I dorsal fin base were minced and homogenized using chloroform and methanol (2:1, v/v) following Folch *et al*. (1957) were prepared in triplicate. Fatty acid methyl esters (FAMEs) were obtained from the lipid extract by using BF_3-methanol (Metcalfe *et al*., 1966).

4.3.4. Gas chromatography: FAMEs were separated by gas-liquid chromatography (Varian CP 3800 U.S.A) equipped with a capillary column (Elite 225, 30 m long and 0.25 mm diameter) and a Flame Ionization Detector (FID) in the presence of hydrogen and air. The carrier gas was nitrogen and the flow rate was 0.5 ml per minute. The chromatograph temperature started at 150^0C and was increased 4^0C min $^{-1}$ until a temperature of 250^0C was attained. Fatty acids separated were identified by the comparison of retention times with those obtained by a separation of a mixture of standard fatty acids. Measurement of peak areas and data processing was done using Star WS software package and the individual

fatty acids were expressed as weight percent of the total fatty acids. Initially one way Analysis of Variance (ANOVA) was performed on the FA composition in relation to sex, season and also the maturity stages within the sexes. To ascertain the impact of these three factors simultaneously along with their interactions in the cases selected based on the above ANOVA, comparison was made using GLM univariate analysis in the statistical package SPSS version 13.0.

4.4. Results

4.4.1. Lipid components and their variations: The polyunsaturated fatty acids (PUFAs) formed the largest component followed by saturated fatty acids (SFA) and monounsaturated fatty acids (MUFA) with a mean of 46.9%, 41.8% and 11% respectively of the total fatty acids in samples pooled irrespective of sex, maturity stage or season (Table. 4.2). None of these three components showed any significant temporal variations ($P > 0.05$). However significant variations ($P<0.05$) were observed with regard to sex where female mackerel had higher levels of SFA compared to males while PUFA levels were higher in males. Among sexes, MUFA level were higher in females but not statistically significant ($P>0.05$). (Table.4.3, Fig.4.1).Within females, significant variation ($P<0.05$) in MUFA content in relation to maturity stages occurred with only 9.1% in immature female compared to 14.1% in mature stages while in males it ranged between 10.2 - 10.7% (Table. 4.4).

Although there were no temporal differences in the total SFA, MUFA and PUFA content of Indian mackerel, certain individual fatty acids within these groups showed variations either in relation to season, sex or maturity stages indicating the dynamics of fatty acid metabolism.

4.4.1.1. Saturated fatty acids (SFA): The average total SFA component of Indian mackerel in the present study was 41.8 % and the dominant fatty acids were Palmitic acid (C16:0, 24.88 %) followed by Stearic acid (C18:0, 9.81 %) and Myristic acid (C14:0, 3.45%) while minor fatty acids included C15:0 and C17:0. The C14:0 and C 16:0 acids were present in significantly ($P<.05$) higher amounts in females as compared to males (Table 4.5; Fig. 4.3 a & b) but did not show any significant differences among the seasons (Table 4.6). However C 15:0 (Pentadecanoic acid) and C17:0 (Heptadecanoic acid) showed significant seasonal differences (Table 4.6; Fig. 4.4 a & b). The SFAs C16:0 and C18:0 did not differ significantly ($P>0.05$) among the maturity stages (Table 4.7).

4.4.1.2. Monounsaturated fatty acids (MUFA): The average total MUFA component of Indian mackerel in the present study was 11.03%. The major MUFAs were oleic acid (C18:1, 6.9%) and Palmitoleic acid (C16:1, 2.9%) while minor components included Eicosenoic (C20:1) and Docosenoic (C22:1) fatty acids.

C 18:1 fatty acid content ranging between 2.03 and 12.34% with a mean of 6.99% was observed (Table 4.2). This FA did not show any significant difference ($P>.05$) among sexes (Table 4.5) but occurred in significantly higher levels ($P<.05$) among mature specimens in both sexes (Table 4.7; Fig. 4.2).

The mean content of C16:1 was 2.95% with significantly higher levels of C16:1 during January (post-monsoon) compared to May (pre-monsoon) period (Table 4.6). Significantly higher levels of C16:1 were observed in females as well as among mature stages of both sexes compared to immature stages (Table 4.7).

The 20:1 and 22:1 FA occurred only in little amounts and did not show any significant seasonal or sex related variations.

4.4.1.3. Polyunsaturated fatty acids (PUFA): Among PUFAs, Docosahexaenoic acid (C22:6n3, DHA- 29.57%), Eicosapentaenoic (C20:5n3, EPA- 6.19%) and Arachidonic acid (C20:4n6, AA- 4.51%) were the major constituents besides Linoleic acid (C18:2n6, 1.92 %) (Table 4.2).

Among PUFAs, DHA which was the single largest component showed significant variations among sex ($P < .05$) (Table 4.5, Fig. 4.3 c) but no significant ($P>.05$) seasonal differences (Table 4.6). EPA was significantly ($P < .05$) lower in females (Table 4.5; Fig. 4.3 d). Among maturity stages, mean levels of both DHA and AA were lower in mature stages compared to immature stages of males and females (Table 4.7).

EPA and AA showed significant ($P<.05$) seasonal variations. While EPA content was higher during January (post-monsoon) compared to May (pre-monsoon), AA levels showed a reverse trend with higher levels during May and lower in January were observed (Table 4.6; Fig. 4.4 d & e). Linoleic acid did not show any significant differences among seasons, sex or maturity stages.

Table.4.2. Mean fatty acid content (%) with standard error (SE) of Indian mackerel of varying maturity stages and all seasons combined.

Fatty acid	mean (%)	Range Minimum	Maximum
C14	3.45 (0.19)	1.84	5.11
C15	1.15 (0.19)	0.64	2.03
C16	24.88 (0.59)	19.9	31.01
C17	1.52 (.08)	0.98	2.43
C18	9.81(0.27)	7.37	12.54
TOTAL SFA	**41.8 (0.66)**	**40.42**	**43.23**
C16:1	2.95 (0.16)	1.72	4.6
C18:1	6.99 (0.54)	2.03	12.34
C20:1	0.39 (0.02)	0.2	0.61
C22:1	0.13 (0.08)	0.07	0.23
TOTAL MUFA	**11.03 (0.18)**	**10.64**	**11.42**
C18:2n6	1.92 (0.018)	1.36	2.46
C20:4n6	4.51 (0.28)	2.05	7.45
C20:5n3	6.19 (0.23)	4.42	8.54
C22:6n3	29.57 (0.80)	22.17	37.64
TOTAL PUFA	**46.9 (0.77)**	**45.32**	**48.59**

Table 4.3. Variations in SFA, MUFA and PUFA levels in relation to seasons and sex

Fatty Acid Group	**Post-monsoon (January)**			**Pre-monsoon (May)**			**Mean**	
	Male	Female	Mean	Male	Female	Mean	Male	Female
SFA	39.9	43.1	41.5	39.5	45.1	42.1	39.7*	44.1*
MUFA	9.3	12.3	10.8	11.7	10.9	11.3	10.5	11.6
PUFA	50.3	44.2	47.4	49.1	43.9	46.5	49.7*	44.1*

(* significant)

Table 4.4. Variations in SFA, MUFA and PUFA levels in relation to maturity stages and sex in *R.kanagurta*

Fatty Acid Group	**Male**		**Female**		**Mean**	
	Immature	Mature	Immature	Mature	Immature	Mature
SFA	40.0	39.1	43.5	44.7	41.8	41.9
MUFA	10.2	10.7	9.1 *	14.1 *	9.7	12.4
PUFA	49.6	50.0	47.2	40.1	48.4	45.5

(* significant)

Table 4.5. Variations in mean content of major fatty acids (% of total fatty acids) of Indian mackerel *R.kanagurta* according to sex.

Fatty acid	Male	Female	Significance F
SFA			
C14:0	2.88	4.02	* F=18.35
C15:0	1.02	1.28	* F=27.38
C16:0	23.20	26.55	* F= 12.52
C18:0	10.07	9.54	NS
MUFA			
C16:1	2.51	3.39	* F=31.30
C18:1n9	6.86	7.12	NS
C20:1	0.41	0.38	NS
C22:1	0.14	0.12	NS
PUFA			
C18:2n6	1.86	1.98	NS
C20:4n6	5.02	4.0	NS
C20:5n3	6.42	5.97	* F= 4.90
C22:6n3	31.68	27.47	* F= 17.3

* significant difference

Table 4.6. Variations in mean content of major fatty acids (% of total fatty acids) of Indian mackerel according to season

Fatty acids	January (Post-monsoon)	May (Pre-monsoon)	Significance (*)
SFA			
C14:0	3.47	3.43	NS
C15:0	0.8	1.49	* F= 34.69
C16:0	24.6	25.1	NS
C17:0	0.98	2.43	* F= 20.78
C18:0	10.07	9.54	* F= 8.29
MUFA			
C16:1	3.3	2.59	* F= 20.36
C18:1n9	6.4	7.58	NS
C20:1	0.2	0.2	NS
C22:1	0.14	0.13	NS
PUFA			
C18:2n6	1.87	1.98	NS
C20:4n6	3.48	5.54	*F= 29.34
C20:5n3	6.9	5.4	*F= 57.7
C22:6n3	30.4	28.68	NS

*- significant difference ; NS= no significant diference

Table 4.7. Mean levels and Standard deviation of select fatty acids among the maturity stages of male and female mackerel (Significant differences if any, indicated by different superscript)

Fatty acid	**Male**		**Female**	
	Immature	***Mature***	***Immature***	***Mature***
C16	23.57 ± 2.34	22.84 ± 2.03	25.37 ± 2.59	27.73 ± 2.26
C18	10.24 ± 1.67	9.90 ±0.72	10.56 ± 1.07	8.52 ± 0.82
C16:1	2.34 ± 0.51	2.67 ± 0.97	3.15 ± 0.51	3.62 ± 0.75
C18:1	6.70 ± 2.00 [a]	7.03 ± 1.39 [b]	4.56 ± 2.60 [a]	9.68 ± 2.03 [b]
C20:1	0.39 ± .03	0.43 ± 0.10	0.45 ± 0.13	0.38 ± 0.14
C22:1	0.113 ± 0.14	0.174 ± 0.05	0.10 ± 0.02	0.13 ± 0.02
C18:2n6	1.86 ± 0.14	1.86 ± 0.13	1.88 ± 0.46	2.09 ± 0.15
C20:4n6	5.148 ± 1.96 [a]	4.90 ± 0.74 [b]	4.66 ± 0.80 [a]	3.34 ± 1.23 [b]
C20:5n3	5.87 ± 1.036 [a]	6.97 ± 1.14 [b]	5.26 ± 0.61 [a]	6.68 ± 1.02 [b]
C22:6n3	31.97 ± 3.90 [a]	31.39 ± 2.27 [b]	30.41 ± 2.27 [c]	24.52 ± 1.81 [d]

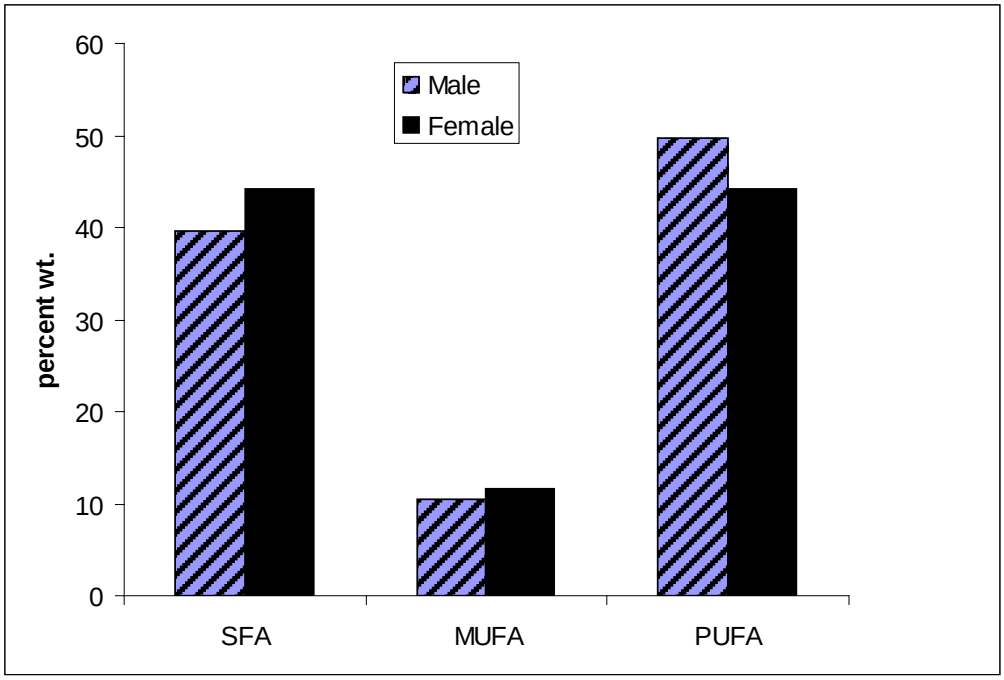


Fig.4.1. Mean Percentage composition of MUFA (P>.05), PUFA (P<.05) and SFA (P<.05) among male and female mackerel

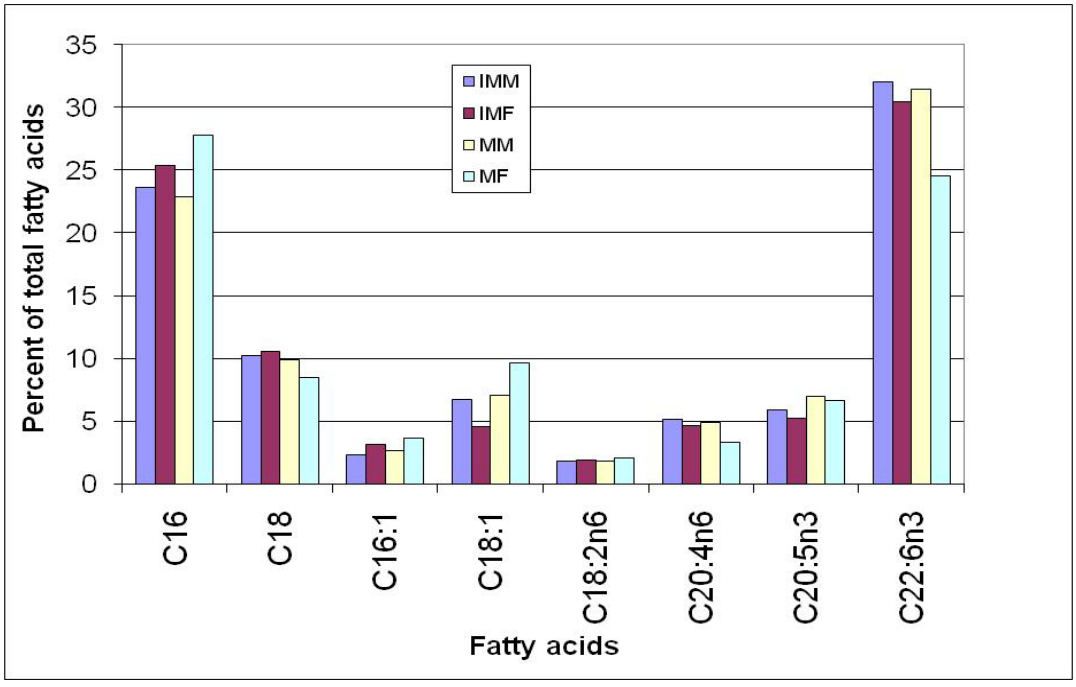


Fig. 4. 2. Relative composition of major SFAs, MUFAs and PUFAs in Indian mackerel (IMM- immature males, IMF- immature females, MM-mature males, MF- mature females)

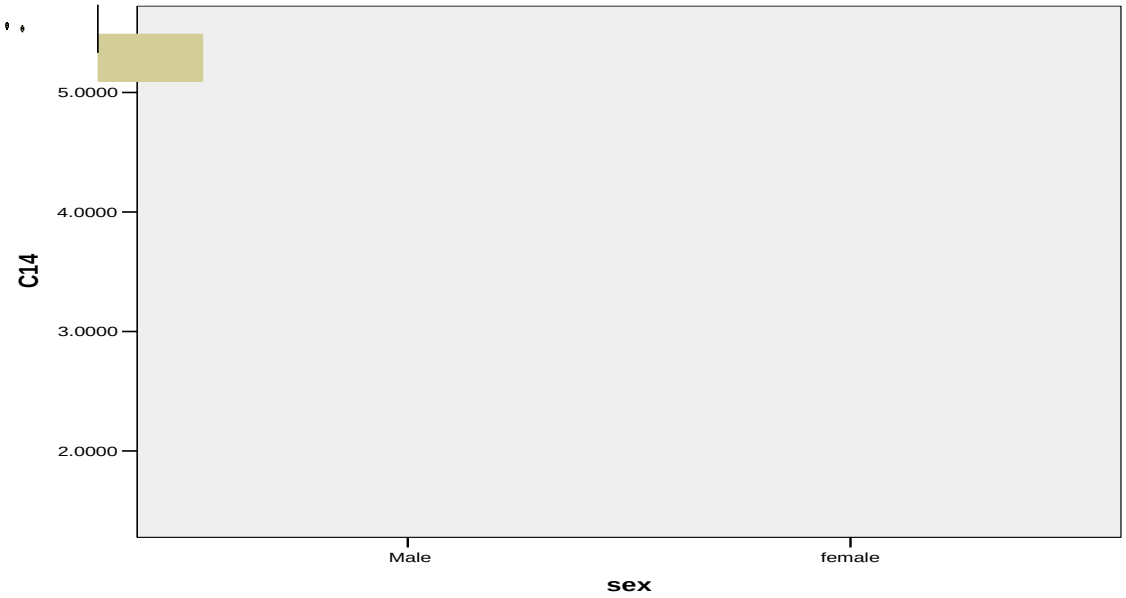


Fig. 4.3a. Boxplots showing median value and standard error of Myristic (C14:0) acid exhibiting significant variations among sexes

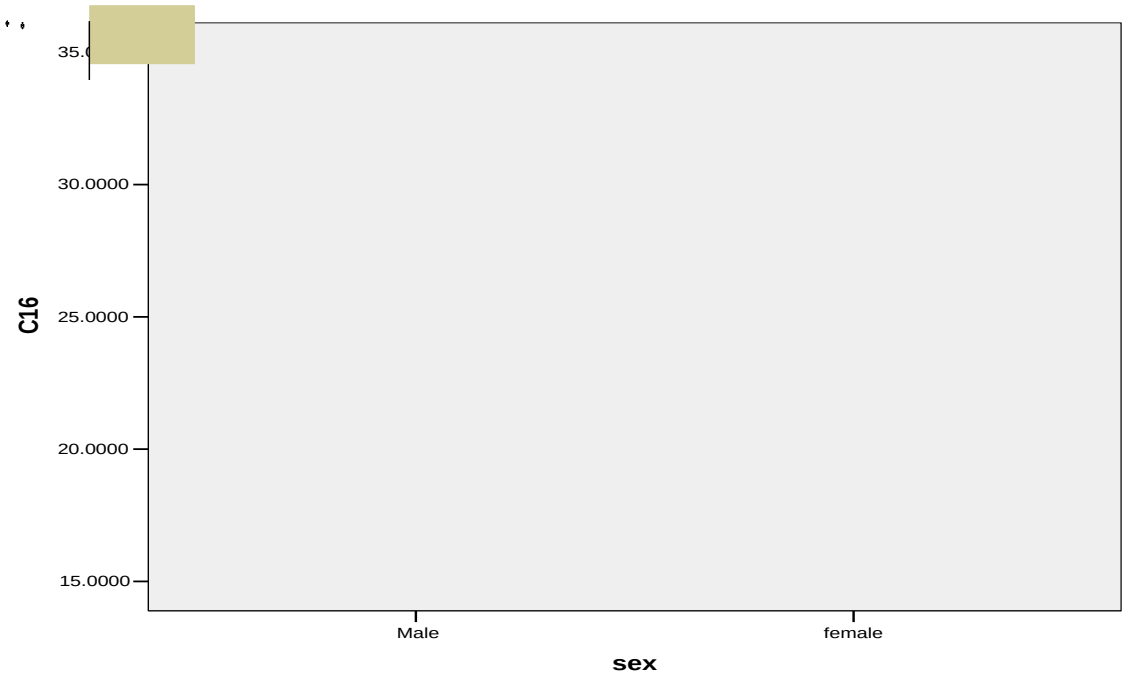


Fig. 4.3 b. Boxplot showing median value and standard error of Palmitic (C16 :0) acid exhibiting significant variations among sexes

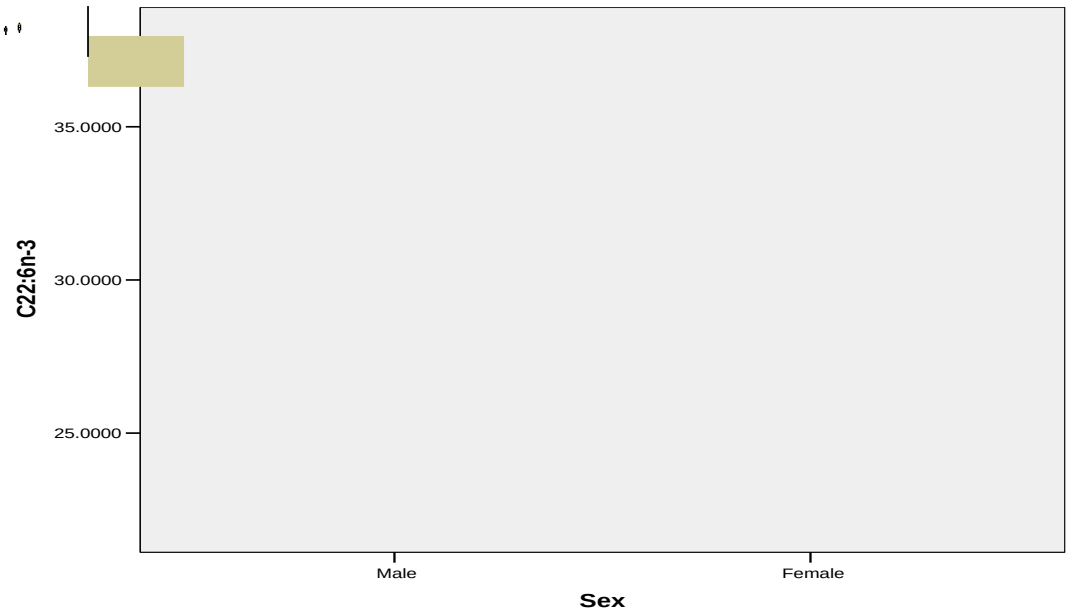


Fig. 4.3 c. Boxplot showing median value and standard error of docosahexaenoic (C 22: 6 n 3) acid exhibiting significant variations among sexes

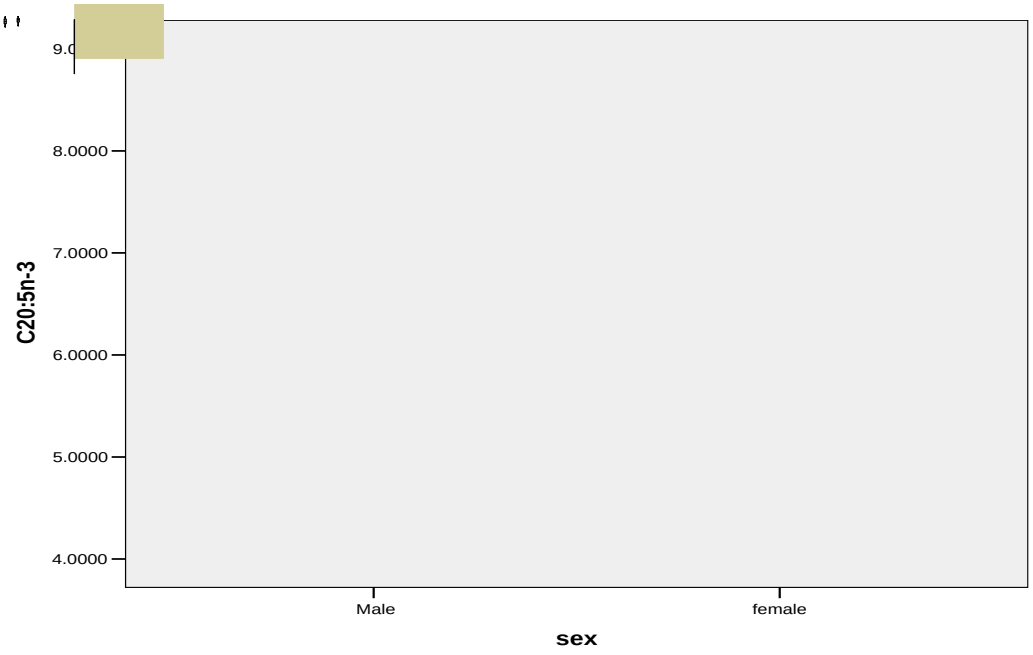


Fig. 4.3 d. Boxplots showing median value and standard error of eicosapentaenoic (C20:5n3) acid exhibiting significant variations among sexes

Fig. 4. 4a. Boxplot showing median value and standard error of pentadecanoic (C15:0) acid exhibiting significant variations among seasons

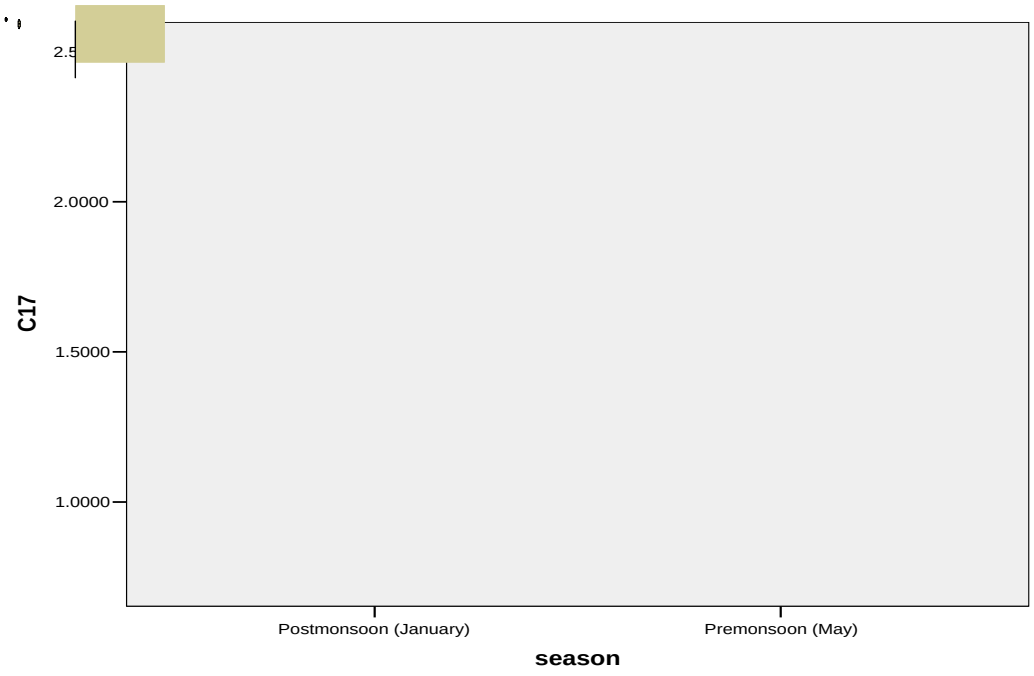


Fig. 4.4 b. Boxplot showing median value and standard error of heptadecanoic (C17:0) acid exhibiting significant variations among seasons

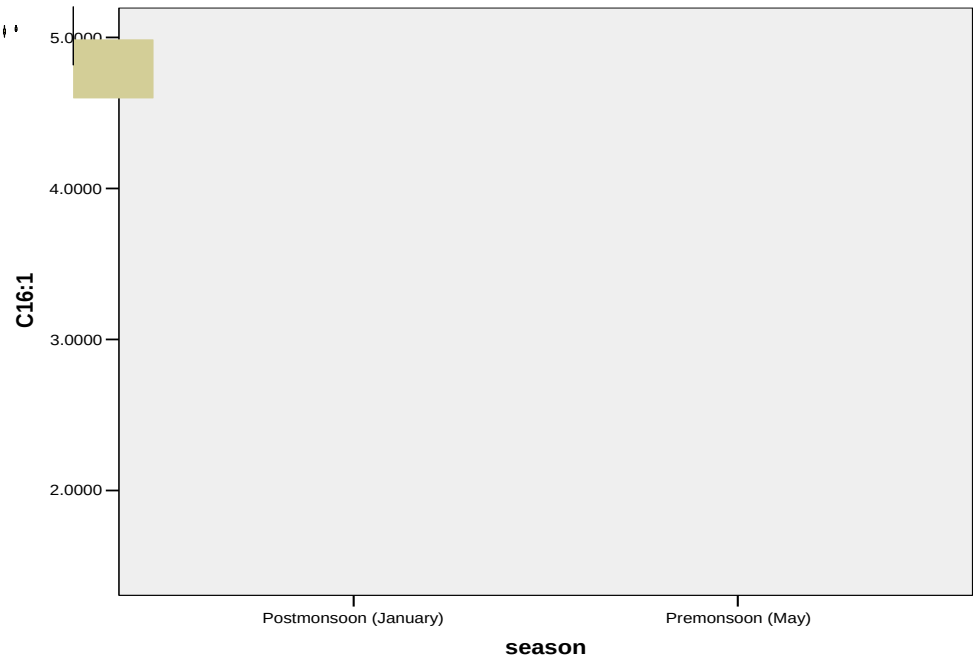


Fig. 4.4 c. Boxplot showing median value and standard error of palmitoleic (C:16n1) acid exhibiting significant seasonal variations

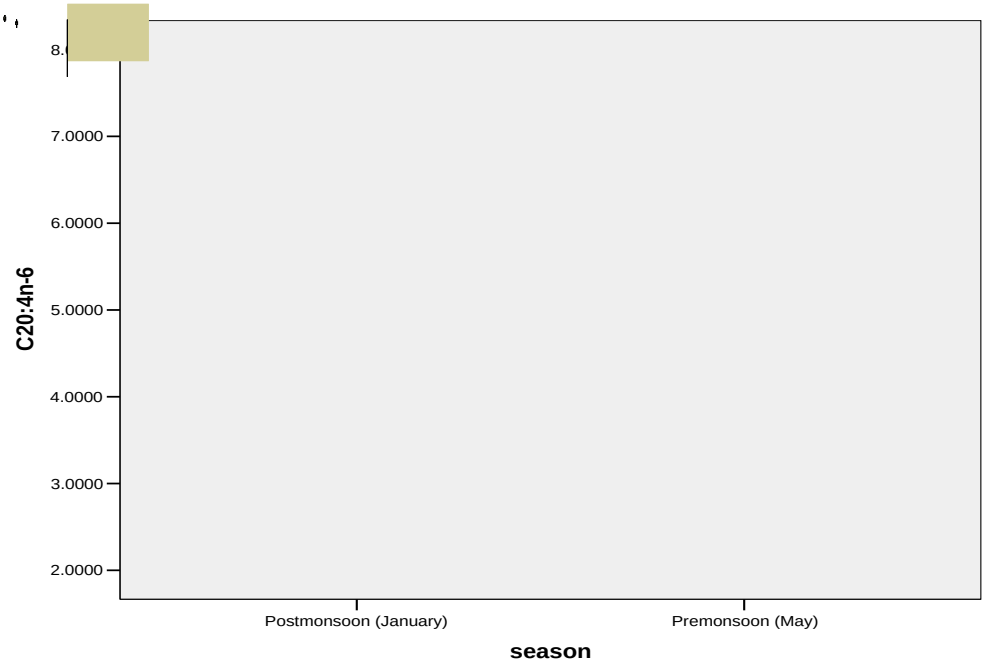


Fig. 4.4 d. Boxplot showing median value and standard error of Arachidonic acid (C20:4n6) exhibiting significant seasonal variations

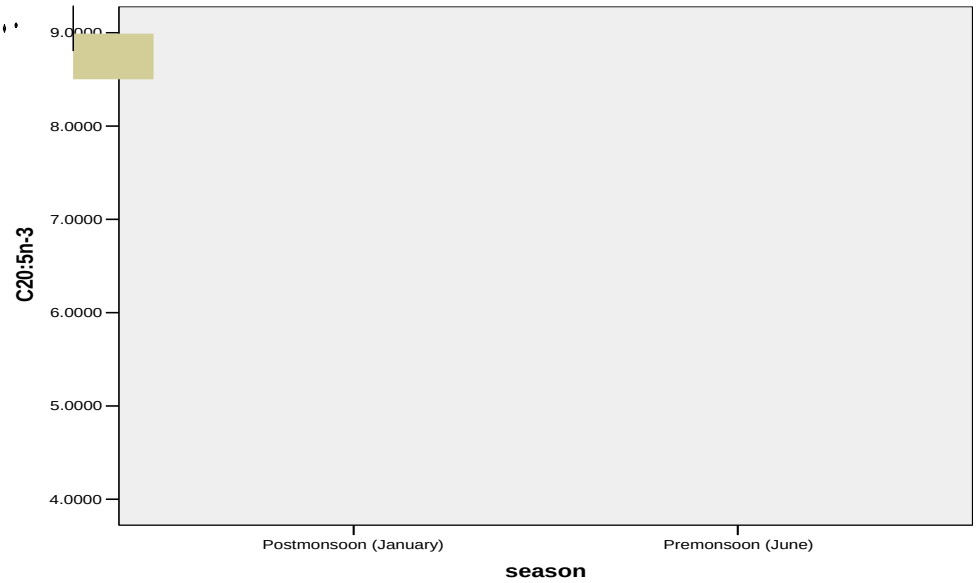


Fig. 4.4 e. Boxplots showing median value and standard error of Eicosapentaenoic (C20:5n3) acid exhibiting significant seasonal variations

4.5 Discussion

4.5.1. Lipid components and their variations: No significant changes in the SFA, MUFA and PUFA contents during January and May months representing the post-monsoon and pre-monsoon seasons respectively were observed in the present study. It has been reported that environment, especially temperature plays a significant role in determining PUFA levels in fish with increasing levels at lower temperatures while MUFAs and SFAs show little variations (Knipparath and Mead, 1966; Bell *et al*., 1986; Saito *et al*., 1997; Farkas *et al*., 2001). The absence of marked seasonal fluctuations in temperature regimes in a tropical marine ecosystem such as Arabian Sea (Longhurst and Pauly, 1987) from which the fish were caught probably precluded seasonal effects on fatty acid composition.

4.5.2. Polyunsaturated Fatty Acids (PUFAs): The PUFA content of Indian mackerel in the present study was high with an average 46.9% although lower than 51.29 % reported for the same species in Malaysian seas (Osman *et al*., 2007). Similar observations of high PUFA levels have been recorded for several marine wild fish from tropical waters (Saito *et al*., 1999; Bayir *et al*., 2006; Osman *et al.,* 2007). Gopakumar (1993) reported higher levels of PUFA in scombroid fishes such as tunas and seerfishes compared with many other common marine food fishes of India. Although the FA of Indian mackerel was not available in this compilation the present study confirms this trend in the Indian mackerel, which also belongs to the family scombridae. Thus, as evident in this study it may be reasonably concluded that although tropical and sub-tropical species are reported to contain lower levels of PUFAs than temperate and sub-arctic species (Ackman, 1989), tropical fishes such as mackerel are also a rich source of PUFAs.

Observations in the present study of high PUFA levels may be indicative of lipid mobilization in Indian mackerel as it is reported that in fishes monoenes and saturated fatty acids are mobilized as energy sources in preference to PUFAs which as a result accumulate in muscle reserves (Kaneko *et al*., 1966; Jeziereka *et al*., 1982; Sidell *et al*., 1995; Tocher, 2003).

4.5.2.a. Docosahexaenoic acid: DHA was the largest component (22.17 – 37.64%) of the total fatty acid composition of Indian mackerel irrespective of the seasons or maturity stages. Observations in the present study agrees with Bayir *et al*. (2006) who reported DHA levels of 10.57 to 34.92% in several marine fish

species in Turkish waters. The results of this study indicates that the Indian mackerel is a rich source of PUFAs, especially DHA.

It is widely believed that fishes are unable to synthesize DHA because of lack of the enzyme 4, 5, desaturase and DHA originates from lipids of prey organisms such as phytoplankton especially dinoflagellates (Kanazawa *et al*., 1979; Sargent *et al*., 1999; Anderson and Pond, 2000). In highly active fishes such as tunas which belong to the family scombridae it has also been attributed to selective catabolism of EPA relative to DHA that results in very high levels of the latter (Watanabe *et al*., 1995; Tocher, 2003). Osaka *et al*. (2006) observed that of all the three *Scomber* species, namely *S. australasicus*, *S. japonicus* and *S.commerson* having similar body sizes, feeding habitat and position in the marine grazing food chain, only the spotted mackerel *S. australasicus* contained comparatively very high (28% of total FA) levels of DHA. They attributed this to the higher energy usage and selective consumption of SFA and MUFA for the offshore migration of this species compared to migrations in coastal water for the other two species. The results of this study indicating DHA as the largest component of the total fatty acids are supported by these observations as mackerel is also known for its migration to deeper waters and is often caught in offshore waters by trawlers (Yohannan and Nair, 2002) as well as feeds on phytoplankton assemblages dominated by dinoflagellates and diatoms (Chapter 3).

High levels of DHA in muscle tissue of females which were lower in mature stages as compared to immature stages noted in the present study. Among PUFAs, DHA is reported to be indispensable for larval growth and survival of

marine fishes (Sargent *et al*., 1999) and selective utilization of fatty acids such as DHA has been reported during the process of yolk deposition in eggs in female gonads (Henderson *et al*., 1984; Wiegand and Idler, 1985; Wiegand 1982; 1996; Kozlova and Khotimchenko, 1993). Thus the results of the present study suggest the mobilization of this important fatty acid from the muscle tissue to the embryos that will be subsequently hatched. It is also in agreement with the observation by Mourente *et al*. (2002) has reported accumulation of DHA in almost all tissues from the very early stages of sexual maturation in tunas and 42.3 fold increase of DHA levels in the ovaries from stage I (immature) to stage IV (mature spawners) of bluefin tuna which was mobilized from the muscle reserves via liver and serum.

4.5.2.b. Eicosapentaenoic acid: EPA constituted 4.42 – 8.54 % of the total FA and was the second largest component among PUFAs. Diatoms which form a significant diet item maybe the source of EPA in mackerel as reported by Brockerhoff *et al*. (1964) especially because seasonal variations were observed that appeared to be related to seasonal diet variations (Chapter 3). The ranking of seasonal food composition based on the I_p (Table 3.3) had indicated diatoms ranked 4^{th} during the post-monsoon season and 6^{th} during the pre-monsoon season. Seasonwise comparison of the fatty acid indicated higher levels during the post-monsoon season *vis-s –vis* the pre-monsoon season. Among sexes also, significantly higher levels were observed in males while the volumetric diet data also indicated higher levels of diatom in the food composition in males (14.3%) compared to females (6.1%) as given in Table 3.6 (chapter 3).

4.5.2.c. Arachidonic acid: AA constituted 2.05 – 7.45 % of the total FA. In general, n6 series of PUFA such as AA are present in negligible amounts in marine fish lipids compared to n-3 PUFA such as EPA and DHA (Ackman, 1989) agreeing with the results of the present study.

AA occurred in significantly lower levels ($P < 0.05$) in mature specimens of both sexes as compared to the immature stages. This fatty acid plays an important role in fish reproduction as precursors of prostaglandins (PG) (Stacey and Goetz, 1982) which have a critical role in ensuring high hatching and fertilization rates for broodstock eggs, promoting growth and survival and improving resistance to acute stress in marine fish larvae (Bell and Sargent, 2003; Johnson, 2009). The observation is supported by Varljen *et al*. (2004) who related seasonal variation in AA levels of *Diplodus vulgaris* to the process of active vitellogenesis and Ballantyne *et al.* (1996) who noted increased levels of AA in the plasma of migrating salmon mobilized from muscle reserves, which was higher among males. However, no differences among the sexes was observed in the present study. It is probable that AA which is considered the principle PG precursor involved in spawning activity of fishes including ovulation and sperm production (Nomura *et al*., 1973; Bell *et al*., 1986; Wade *et al*., 1994) and reported to be specifically concentrated in fish eggs and sperms after being mobilized from the muscle tissues (Tocher and Sargent, 1984; Bell *et al*., 1996) is found in lower levels in mature specimens of both sexes indicating its increased mobilization from the muscle tissue.

AA has been identified as a marker of macroalgae and seaweeds in the diets of fishes (Nichols *et al*., 1986; Osako *et al*., 2006a; Saito *et al*., 1999) . In the present study significant (P<.05) seasonal differences in the levels of AA were observed while feeding preferences indicated algae is a significant contributor to the diet composition during the pre-monsoon period (chapter 3) and this may be the reason for the higher levels observed in samples collected in the month of May.

4.5.2 d. DHA: EPA ratio: The DHA: EPA ratios indicated higher levels of DHA compared to EPA which was contrary to that observed in sardines (*Sardinella* spp.) where EPA content was higher (Gopakumar, 1993; Njinkoue *et al*., 2002). This difference in the EPA and DHA content of the two species *R. kanagurta* and *S. longiceps* which share the same pelagic habitats are presumably due to the differences in their diet dominated by zooplankton such as copepods and phytoplankton (mainly diatoms) respectively (Vivekanandan *et al*., 2009; Sivadas and Bhaskaran, 2009). Diatoms are reported to preferentially synthesize EPA at high levels (Ackman *et al*., 1968) and various studies have indicated that a fish diet dominated by diatoms is likely to show dominance of EPA over DHA (Ackman *et al*., 1964; Hayashi and Takagi, 1977; Gooch *et al*., 1987; Edirsinghe *et al*., 1998; Sigurgisladottir and Palmadottir, 1993). The DHA: EPA ratio of the Indian mackerel in this study was 4.7. In scombroid fishes such as tunas, ratios of 3.4 to 5.8 for Pacific northern bluefin tuna (Ishihara and Saito, 1996) and 7.4 and 11.3 for the Atlantic northern bluefin (*Thunnus thynnus*) and yellowfin (*T.albacares*) was reported by Medina *et al.* (1995) which is similar to the Indian mackerel, another scombroid fish.

4.5.3. SFAs: SFA accounted for 41.8% of the total fatty acids and Palmitic acid (C16:0, 24.8%) and Stearic acid (C18:0, 9.8%) were the major components. The SFAs noted in the present study indicate that it probably originated from the copepod dominated diet of mackerel (chapter 3) which is supported by the observations of Ratnayake and Ackman (1979) that important saturated fatty alcohols of copepods such as C14:0, 16:0, 18:0 as well as minor components such as 15:0 and 17:0 are present in similar proportions in fishes feeding on them indicating the dietary source of these FA. The C18:0 FA showed significant seasonal differences among the two seasons (post- monsoon season and pre-monsoon) coinciding with higher contribution by copepods to the diet of mackerel during the post- monsoon season (% I_p= 39.29) compared to pre-monsoon season (%I_p= 16.89) (Chapter 3) which probably results in the differences. However, Palmitic acid which was another major FA component among SFAs did not show pronounced seasonal variations probably because copepods are the major dietary source of this FA and forms a food item in all the seasons, thereby agreeing with observation made by Gallagher *et al*. (1989), Bayir *et al*. (2006) and Recks and Seaborn (2008).

The presence of minor FA such as C15:0 and C17:0 which occurred significantly higher (P<.05) during the pre-monsoon season compared to post-monsoon period is probably related to seasonal variations in the detritus content of mackerel diet (chapter 3) as these FA have been used in marine food web studies to identify food sources such as bacterial biomass/detritus (Meziane and Tsuchiya, 2000; Wilson *et al*., 2001). Madhupratap *et al*. (2001) and Smith and Madhupratap

(2005) have indicated that there is a large build-up of dissolved organic carbon (DOC) in the Arabian sea during the pre-monsoon season which leads to growth of bacterial population as well as microzooplankton which in turn are fed by copepods and these in turn by fishes which confirms and highlights the importance of diet in determining fatty acid composition of mackerel. C15:0 and C17:0 variations were recorded by in his study on fatty acid profiles of detritivorous reef fishes while Recks and Seaborn (2008) related short chain fatty acids such as C14:0 and C15:0 in mullet to its omnivorous feeding habit on microalgae, macrophyte detritus and inorganic sediment rich in absorbed micro-organisms. The results of this study thus indicate that there is significant effect of diet on mackerel FA composition.

4.5.4. MUFAs: The study agrees with other studies where comparatively high levels of monoenoic fats are reported in pelagic fishes such as capelin (*Mallotus villosus*), Henderson *et al*., 1984; herring (*Clupea harengus*) Tocher *et al*., 1985; Linko *et al*., 1985; sprats (*Sprattus sprattus*) Hardy and Mackie, 1969; saury (*Cololabis saira*) Ota *et al*., 1980).

The higher levels of MUFA in female mackerel is in agreement with the observations of Wiegand and Idler (1985) and Ballantyne *et al*. (1996) of progressively higher levels of monoenoic acids coinciding with the development of ovaries and increase in the gonado-somatic index of Atlantic salmon *Salmo salar* and sockeye salmon *Oncorhynchus nerka* respectively during their spawning migrations. Studies on the Arctic charr *Salvelinus alpinus* (L.) by Jorgensen *et al*., (1997) also suggest gender – related differences in spawning investment which is predominantly the monoenoic lipid reserves. Among MUFAs only C16:1 showed

significant differences among sexes being significantly lower among female mackerel. The conclusions drawn by Henderson *et al*. (1984) that in certain fishes females catabolise more monoenoic fatty acids than males during sexual maturation support this observation in *R. kanagurta*.

Monoenoic fatty acids of Indian mackerel probably originate from the copepods which form the most important food item as studied by diet composition (chapter 3). In most marine species of fish, natural diets are a good source of fatty acids (Tocher, 2003) and it is reported that in fishes such as herring, menhaden and capelin a copepod diet rich in wax esters and triglycerides are assimilated efficiently and directly converted into the monoenoic fatty acids such as C16:1 and C18:1 and C20:1 and C 22:1 FA (Ratnayake and Ackman, 1979) resulting in their high levels in muscle tissues. However in the present study very low levels of 20:1 and 22:1 FA was recorded which was similar to observations of Kas'yanov *et al*. (2002) in the fish Anadyr capelin which also predominantly feeds on copepods.

The observation of omnivorous feeding behaviour and diet composition which indicates inclusion of algal matter, copepods, crustaceans and detritus in the present study (chapter 3) is consistent with fatty acids estimated in muscle tissue in the present study and their potential sources mentioned in the literature. The study by Kirsch *et al.* (1998) on cod fed prey items such as squid and mackerel that differed significantly in their fat content and fatty acid composition indicated that deposition of dietary fatty acids is integrated over a period of two to three weeks and probably holds true for all fishes including the Indian mackerel. The present study also indicated several individual fatty acids showing variations and were

probably influenced by feed consumed as well as physiological factors such as maturation patterns. It is therefore suggested that further detailed investigations of the fatty acid profile of Indian mackerel and also several other commercially important species sharing its habitat will aid in identifying fatty acids which can be used as markers in ecological studies as well as understanding the feeding dynamics of the resource.

****

CHAPTER 5
SUMMARY AND CONCLUSIONS

CHAPTER 5

SUMMARY AND CONCLUSIONS

The Indian mackerel forms a major fishery resource by itself in the Indian marine fisheries sector. A characteristic of the mackerel fishery is the highly fluctuating nature of the catches over interannual / decadal scales which has been attributed to fishery as well as non-fishery factors. Most of the studies to present date are during the period prior to 80s and from the North Kerala/Karnataka belt. There is intimate relation between feeding, its cycling for gonadal and somatic growth processes and subsequent recruitment success. The present study therefore was aimed at understanding the dynamics of the *R.kanagurta* resource using a holistic approach integrating information on the maturation, feeding and lipid dynamics from a relatively less studied region, namely, the Central Kerala coast.

The present study indicated that there is no population synchrony in spawning of Indian mackerel resulting in the availability of spawners throughout the year. But it is clear that from the availability of the various stages of maturity during the various months maximum spawning activity occurs during the late pre-monsoon and early monsoon period (May -June) and a small minor peak occurs during November which is probably due to the favorable environmental conditions and food availability during these periods. The fishery along the central Kerala coast is thus mainly sustained by the recruits originating around May and November.

The macroscopic gonad staging method is the most simple and rapid method in obtaining data on maturity and spawning which are inputs in routine fish stock assessment studies. Most of the present studies employ a 7-8 stage classification system which are based on maturation keys basically developed for temperate water species. However the reproductive strategies of tropical fishes such as mackerel are found to be much different from temperate water species. A simplified Key using 4 maturation stages of mackerel taking into consideration the GSI and ova-diameter distribution was developed which was validated using histological tools. This scale was found to be more reliable than those based only on either gross appearance or ova-diameter measurements alone. This method therefore can be tested in samples over temporal/geographical scale and modifications if any required, may be included and used subsequently for routine macroscopic gonad staging. Adoption of such a scale can also facilitate comparisons among studies conducted over temporal or geographical scales in future and also enable utilization of historical databases already available.

This study indicates that apparently there has been no major change in the spawning /maturation schedules of Indian mackerel along the southwest coast of India unlike in some other resources where deviations attributed to recent shifts in climate are reported. This may perhaps be due to the fact that the mackerel is already placed in a favorable environmental window and therefore such “shifts” are not evident. However, the L_m of mackerel showed much variation during the period and was lower than that reported during the period prior to the 90s. In the context of an expanding mackerel fishery attributed to

increasing seawater temperature due to climate-change, the study indicates that an evaluation of the historic database on the maturation/spawning of mackerel may be interesting to evaluate the same with regards to the fishery biology of mackerel.

The study also indicated that the fecundity levels being related to the total length of the fish, the effects of recruitment overfishing (large scale capture of mature spawners) are likely to be a significant factor in determining recruitment variations. At present, capture of juvenile fishes only is discouraged and hence management advisories may also consider conservation of spawners, especially during the pre-monsoon period and those in the size group 200 - 240 mm. It may be mentioned that presently most of the large sized fish (>220 mm) caught in trawls are fishes that are in spent condition and their fishing may not be a threat. However any fishery that specifically targets large spawners such as the seasonal gill net fishery operated during dusk off Calicut coast reported by Yohannan (1997) and similar fisheries elsewhere, if any, are more likely to be an unsustainable method of fishing which can be discouraged.

Generalised, rapid and opportunistic feeding behaviour, strong preference for copepods and the strategic utilisation of all available resources including detritus was indicated in the study. The study revealed that detritus was a major food item during the pre-monsoon period which also coincides with its spawning peak. The early views that detritus is ingested along with other food items accidentally and forms only an insignificant part of diet may thus be partly responsible for oversight of detritus as a food source for omnivores such as

mackerel. Hence more detailed qualitative analysis of gut contents combined with studies using more advanced methods to study time-integrated assimilated diets and energy transfer may be attempted. Such studies for all major fishery resources in the region can be used for developing ecosystem models that can play important role in fisheries management.

The present study indicates that PUFA content of Indian mackerel study was high with an average 46.9% of the total fatty acids and also is a rich source of DHA. The present study also indicated several individual fatty acids showing variations indicating possible relationship with the maturation and feeding patterns. Some of the important observations include significantly higher levels of DHA as compared to EPA related to a feeding preference for copepods rather than diatoms and seasonal variations in SFAs such as C18:0, C15:0 and C 17:0 related to habitat shifts associated diet changes. It is therefore suggested that further detailed investigations of the fatty acid profile of Indian mackerel and also several other commercially important species sharing its habitat will aid in identifying fatty acids which can be used as markers in ecological studies as well as understanding the feeding dynamics of the resources. Changes in certain fatty acids like DHA and AA in relation to maturity stages indicating their mobilization pattern observed in the present study are also likely to be useful in understanding the diet-modulation of reproduction and its possible effects on recruitment to the fishery subsequently.

****

REFERENCES

REFERENCES

Abdussamad, E. M., H. M. Kasim and P. Achayya. 2006. Fishery and population characteristics of Indian mackerel, *Rastrelliger kanagurta* (Cuvier) at Kakinada. *Indian. J. Fish*., 53(1): 77 – 83.

Ackman, R. G. 1980. Fish lipids *In*: Connell, J.J. (Ed.) *Advances in Fish Science and Technology*, Farnham England: Fishing News Books, pp. 87 -103.

Ackman, R. G. 1982. Fatty acid composition of fish oils. *In*: Barlow, S. M. and M. E. Stansby (Eds.). *Nutritional evaluation of long-chain fatty acids in fish oil*. Academic Press, New York, pp. 25 – 88.

Ackman, R. G. 1989. Fatty acids. *In*: R.G.Ackman (Ed.) *Marine Biogenic Lipids, Fats and Oils*, CRC Press, 145 -178.

Ackman, R. G., P. M. Jangaard, R. J. Hoyle and H. Brockerhoff. 1964. Origin of marine fatty acids. I. Analyses of the fatty acids produced by the diatom *Skeletonema costatum*. *J. Fish. Res. Bd. Can*., 21: 747 -756.

Ackman, R. G., M. N. Ratnayake and C. A. Eaton.1981. Considerations of fatty acids in Menhaden from the northern limits of the species. *Proc. N. S. Inst. Sci*., 31: 207 – 217.

Ackman, R. G., C. S. Tocher, J. McLachlan. 1968. Marine Phytoplankter fatty acids. *J. Fish. Res. Bd. Can*., 25: 1603 – 1620.

Ackman, R. G., J. L. Sebedio and M. I. P. Kovacs. 1980. Role of eicosenoic and docosenoic fatty acids in freshwater and marine lipids. *Mar. Chem.*, 9: 157 – 164.

Adams, P. B. 1980. Life history patterns in marine fishes and their consequences for fisheries management. *Fish. Bull*., 78 : 1 – 12.

Agnalt, A-L. 2006. Long term changes in growth and age at maturity of mackerel *Scomber scombrus* L., from the North Sea. *J. Fish Biol*., 35: 305 – 311.

Ahlgren, M. O. 1996. Selective ingestion of detritus by a north temperate omnivorous fish, the juvenile white sucker, *Catostomus commersoni*. *Env. Biol. Fish*., 46 (4): 375 – 381.

Alekseev, F. E. , E. P. Alekseeva and M.E. Grudtsev. 1989. Some aspects of the reproductive biology of flying fishes of the genus *Exocetus* of the Atlantic Ocean. *J. Ichthyol.,* 29(4): 50 – 61.

Alheit, J. 1989. Comparative spawning biology of anchovies, sardines and sprats. *In*: Blaxter, J.H.S, J.C. Gamble and H. vonWesternhagen (Eds.) *The early life history of Fish*, p. 7 – 14.

Anderson, T.R., and D.W.Pond. 2000. Stoichiometric theory extended to micronutrients: Comparison of the roles of essential fatty acids, carbon and nitrogen in the nutrition of marine copepods. *Limnol. Oceanogr*., 45 (5): 162 - 167.

Annigeri, G.G. 1963. Maturation of the intra-ovarian eggs and the spawning periodicities in few fishes of the mangalore area based on ova-diameter measurements. *Indian J. Fish*., 16: 35 – 50.

Anon., 1976. Plankton, fish eggs and larvae studies. UNDP/FAO Pelagic Fishery Project (IND/69/593), Progress report no. 17, 27p.

Antony Raja, B.T. 1964. Some aspects of spawning biology of Indian oil sardine *Sardinella longiceps* Val. *Indian J. Fish*., 11A: 45 – 120.

Antony Raja, B.T. 1971. On the maturity stages of Indian oil-sardine *Sardinella longiceps* Val. with notes on incidence of atretic follicles in advanced ovaries. *Indian J. Fish*., 13 : 27 – 47 (1966).

Antony Raja, B.T. 1971a. Fecundity fluctuations in the oil-sardine *Sardinella longiceps* Val. *Indian J. Fish*., 18 (1& 2): 84 – 98.

Antony Raja, B. T. and V. N. Bande. 1972. An instance of abnormally ripe ovaries in the Indian mackerel , *Rastrelliger kanagurta* (Cuvier). *Indian J. Fish*., 19 (1&2): 176 – 179.

Aoki, T., K. Takada and N. Kunisaki. 1991. On the study of proximate composition, mineral, fatty acid, free amino acid, muscle hardness and color differences of six species of wild and cultured fishes. *Nippon Suisan Gakkaishi*, 57: 1927 – 1934.

Appa Rao, T. 1964. Maturity and spawning habits of some sciaenids in offshore waters of Visakhapatnam. *Indian J. Fish*., 11 (1): 121 – 126.

Appa Rao, T. 1967. Fat and water contents of the muscle and ovary during the maturation cycle of *Pseudosciaena aneus* and *Johnius carutta* (Bloch) *Indian J. Fish*., 14: 293 –297.

Armstrong, M.J.P., P. Connolly, R. D. M. Nash, M.G. Pawson, E. Alesworth, P. J. Coulahan, M. Dickey Collas, S.P. Milligan, M.F.O'Neill, P. R.Witthames and L.Woolner. 2001. An application of the annual egg production method to estimate the spawning biomass of cod (*Gadus morhua*), plaice (*Pleuronectes platessa* L.) and sole (*Solea solea* L.) in the Irish Sea. *ICES J. Mar. Sci*., 58: 183 – 203.

Arocha, F. 2002. Oocyte development and maturity classification of swordfish from the north-western Atlantic*. J. Fish Biol*., 60: 13 – 27.

Asokan P. K., P. K. Krishnakumar and S. Ghosh. 2009. Sea surface temperature changes and distribution shifts of Indian mackerel *Rastrelliger kanagurta*. In: *Marine Ecosystems Challenges and Opportunities*, *Book of Abstracts* (Ed. E.Vivekanandan *et al*.), Marine Biological Association of India, February, 9- 12, 2009, Cochin, p. 247 – 248.

Bagarinao, T. and T. E. Chua. 1986. Egg size and larval size among teleosts: Implications to survival potential. *In*: J.L. Maclean, L.B. Dizon and L.V. Hosillos (Eds.) *The First Asian Fisheries Forum*, Asian Fisheries Society, Manila, Phillipines, p. 651 – 656.

Bagenal, T. B. 1966. The ecological and geographical aspects of the fecundity of the plaice *J. Mar. Biol. Ass. U.K*. 46: 161 – 186.

Bagenal, T. B. 1978. Aspects of fish fecundity. *In*: S.D.Gerking (Ed.) *Ecology of freshwater fish production*. Third edition, Blackwell, Oxform, p. 75 – 101.

Ballantyne, J. S., F. Mercure, M. F. Gerrits, G. VanDerKraak, S. McKinley, D. W. Martens, S. G. Hinch and R. E. Diewer. 1996. Plasma nonesterified fatty acid profiles in male and female sockeye salmon *Oncorhynchus nerka* during the spawning migration. *Can. J. Fish. Aquat. Sci.*, 53: 1418 – 1426.

Balon, E.K.. 1984. Patterns in the evolution of reproductive styles in fishes. *In*: G. W. Potts and R.G. Wootton (Eds.) *Fish Reproduction: Strategies and tactics*. Academic Press, New York, p. 35 – 53.

Bandarra, N. M., I. Batista, M. L. Nunes, J. M. Empis and W. W. Christie. 1997. Seasonal changes in the lipid composition of sardine (*Sardina pilchardus*). *J. Food Sci*., 62: 40 – 42.

Bandarra, N. M., I. Batista, M. L. Nunes and J. M. Empis. 2001. Seasonal variation in the chemical composition of horse mackerel (*Trachurus trachurus*). *Euro Food Res Technol*., 212: 535 – 539.

Bayir, A., Haliloglu, H. I., A. N. Sirkecioglu and N. M. Aras. 2006. Fatty acid composition in some selected marine fish species living in Turkish waters. *J. Sci. Food Agric*., 86: 163 -168.

Begg, G. A., J. A. Hare and D. D. Sheehan. 1999. The role of life-history parameters as indicators of stock structure. *Fish. Res*., 43: 141 – 163.

Begg, G. A. and J. R. Waldman. 1999. An holistic approach to fish stock identification. *Fish. Res*., 43: 35 – 44.

Bell, J. G. and J. R. Sargent. 2003. Arachidonic acid in aquaculture feeds: current status and future opportunities. *Aquaculture*, 218: 491 – 499.

Bell, M.V., J. R. Dick, M. Thrush, J. C. Navarro. 1996. Decreased 20:4n6 / 20:5n3 ratio in sperm from cultured sea bass, *Dicentrarchus labrax*, broodstock compared with wild fish. *Aquaculture* 144: 189 – 199.

Bell, M. V. and J. R. Sargent. 1996. Lipid nutrition and fish recruitment. *Mar. Ecol. Prog. Ser.*, 164: 315 – 316.

Bell, M.V., R. J. Henderson and J. R. Sargent. 1986. The role of polyunsaturated fatty acids in fish. *Comp. Biochem. Physiol.,* 83 B: 711 –719.

Belling, G. B., M. Abbey, J. H. Campbell and G. R. Campbell. 1997. Lipid content and fatty acid composition of 11 species of Queensland (Australia) fish. *Lipids*, 32 (2): 621 – 626.

Benavides, A. G., J. M. Cancino and F. P. Ojeda. 1994. Ontogenetic changes in gut dimensions and macroalgal digestibility in the marine herbivorous fish, *Aplodactylus punctatus*. *Functional Ecology*, 8: 46 -51.

Bengston, D. A., R. C. Barkman and W. J. Berry. 1987. Relationships between maternal size, egg diameter, time of spawning season, temperature, and length at hatch of Atlantic silverside, *Menidia menidia*. *J. Fish Biol*., 31: 697 – 704.

Berg, J. 1979. Discussion of methods of investigating the food of fishes, with reference to a preliminary study of the prey of *Gobiusculus flavescens* (Gobiidae). *Mar. Biol*., 50: 263 - 273

Beverton, R. J. H. 1992. Patterns of reproductive strategy parameters in some marine teleost fishes. *J. Fish. Biol*., 41(5): 137 – 159.

Beverton, R . J. and S. J. Holt. 1957. *On the dynamics of exploited fish populations*. Fisheries Investigation Series II, vol. 19, 533 pp. (Reprinted 1993, Blackburn Press, Caldwell, NJ,USA).

Bhimachar, S. and P.C. George. 1952. Observations on the food and feeding of Indian mackerel *Rastrelliger kanagurta* (Cuvier). *Proc. Indian Acad. Sci*., 36B (3): 105 – 117.

Bishop, D. G., D. G. James and J . Olley. 1976. Lipid composition of slender tuna *Allothunnnus fallai*) as related to lipid composition of their feed (*Nyctiphanes australis*). *J. Fish. Res. Bd. Can.,* 33: 1156 – 1161.

Blanchard, J.L., K.T. Frank and J.E. Simon. 2003. Effects of condition on fecundity and total egg production of eastern Scotian shelf haddock (*Melanogrammus aeglefinus*). *Can. J. Fish. Aquat. Sci*., 60(3): 321-332.

Blaxter, J. H. S. 1986. Development of sense organs and behavior of teleost larvae with special reference to feeding and predator avoidance. *Trans. Am. Fish. Soc*., 115 : 98 – 114.

Blaxter, J. H. S. and G. Hempel. 1963. The influence of egg size on herring larvae. *J. du Conseil, Conseil International pour l'exploration de la mer*., 28: 211 – 240.

Blaxter, J. H. S. and J. R. Hunter, 1982. The biology of the clupeoid fishes. *In*: Blaxter, J.H.S., F.S. Rusell and M. Yonge (Eds.). *Advances in Marine Biology*, Vol. 20: 3 – 194.

Bleil, M and R. Oeberst. 2005. The potential fecundity of cod in the Baltic sea from 1993 to 1999. *J. Appl. Ichthyol.* 21: 19 – 27.

Bowen, S. H. 1979. A nutritional constraint in detritivory by fishes: the stunted population of *Sarotherodon mossambicus* in lake Sibaya, South Africa. *Ecological Monographs*, 49(1): 17 -31.

Bowen, S.H. 1981. Digestion and assimilation of periphytic detrital aggregate by *Tilapia mossambica*. *Trans. Am. Fish. Soc*., 110 : 239 – 245.

Bowen, S.H. 1984.Evidence of a detritus food chain based on consumption of organic precipitates. *Bull. Mar. Sci*., 35: 440 – 448.

Bowen, S. H., E. V. Lutz and M .O. Ahlgren, 1995. Dietary protein and energy as determinants of food quality: trophic strategies compared. *Ecology*, 76(3): 899 – 907.

Bowering, W. R. 1989. Witch flounder distribution off southern Newfoundland, and changes in age, growth and sexual maturity patterns with commercial exploitation. *Trans. Am. Fish. Soc*., 118: 659 – 669.

Brockerhoff, H., M. Yurkowski, R. J. Hoyle and R.G. Ackman. 1964. Fatty acid distribution in the lipids of marine plankton. *J. Fish. Res. Bd. Canada*, 21 (6): 1379 – 1384.

Bromage, N. R. and R. J. Roberts (Eds.) 1995. *Broodstock management and Egg and Larval Quality*. Oxford: Blackwell Science, New York.

Brooks, S., C.R. Tyler and J. P. Sumpter. 1997. Egg quality in fish: what makes a good egg? *Rev. Fish. Biol. fish*., 7: 387 – 416.

Bruce, M., F. Oyen, G. Bell, J. F. Austriano, B. Farndale, M. Carrillo, S. Zanuy, J. Ramos and N. Bromage. 1999. Development of broodstock diets for the European sea bass (*Dicentrarchus labrax*) with special emphasis of the importance of n-3 and n-6 highly unsaturated fatty acid to aquaculture performance. *Aquaculture* 177: 85

Budge, S. M., S. J. Iverson, W. D. Bowen, R. G. Ackman. 2002. Among and within-species variability in fatty acid signatures of marine fish and invertebrates on the Scotian Shelf, Georges Bank and southern Gulf of St.Lawrence. *Can.J. Fish. Aquat. Sci*., 59: 886 – 898.

Cailliet, G. M., M. Love and A.W. Ebling. 1986. *Fishes: A field and laboratory manual on their structure, identification and natural history*. Wadsworth Press, Belmont, CA, 194 p.

Cayre, P. and F. Laloe 1986. Review of the gonad index (GI) and an introduction to the concept of its 'critical value' : application to the skipjack tuna, *Katsuwonus pelamis*, in the Atlantic Ocean. *Mar. Biol.,* **90** : 345-51.

Cejas, J.R., E. Almansa, J. E.Villamandos, P. Baslia, A. Bolanos and A. Lorenzo. 2003. Lipid and fatty acid composition of ovaries from wild fish and eggs from captive fish of white sea bream, *Diplodus argus*. *Aquaculture*, 216: 299- 313

Chambers, C. R. and K. G. Walwood. 1996. Maternal and seasonal difference in egg sizes and spawning characteristics of captive Atlantic cod, *Gadus morhua*. *Can. J. Fish. Aquat. Sci.,*53: 1986 – 2003.

Chidambaram, K. 1944. Food of the Indian mackerel *Rastrelliger kanagurta* (Russell) of the west coast of Madras Presidency. *Curr.Sci.,* 13(8) 214 -215.

Chidambaram, K., C. G. Krishnamurthy, R.Venkataraman and S.T.Chari. 1952. Studies on mackerel : Fat variation and certain biological aspects. *Proc. Indian Acad. Sci*., 35B(2): 43 –68.

Childress, J. J., S. M. Taylor, G. M . Cailliet and M. H. Price. 1980. Patterns of growth, energy utilisation and reproduction in some meso and bathy pelagic fishes of southern California. *Mar. Biol.,* 61 : 27 –40.

Ciechomskii, J.D. and D. A. Capezaani, 1969. Fecundity of the Argentinian mackerel *Scomber japonicus marplatensis*. *Mar. Biol*., 2: 277 – 282.

Clark, F. N. 1934. Maturity of the Californian sardine (*Sardina caerulea*) determined by ova-diameter measurements. *Calif. Dep. Fish & Game, Fish Bull*., 12: 59 pp.

Clarke, T.A. 1987. Fecundity and spawning frequency of the Hawaiian anchovy or Nehu, *Encrasicholina purpurea*. *Fish. Bull*., 85 (1): 127 – 138.

Clarke, A. and L. J. Holmes, 1986. Lipid content and composition of some midwater crustaceans from the Southern Ocean. *J. Exp. Mar. Biol. Ecol*., 31 -51.

Coates, D. 1988. Length-dependent changes in egg size and fecundity in females, and brooded embryo size in males, of fork-tailed catfishes (Pisces: Ariidae) from the Sepik River, Papua New Guinea, with some implications for stock assessments. *J. Fish Biol*., 33: 455 – 464.

Connover, D.O. 1985. Field and laboratory assessment of patterns in fecundity of a multiple spawning fish: the Atlantic silverside *Menidia menidia*. *Fish. Bull*., 83(3): 331 – 341.

Correia, A. M. 2002. Niche breadth and trophic diversity: feeding behaviour of the red swamp crayfish (*Procambrus clarkii*) towards environmental availability of aquatic macroinvertebrates in a rice field (Portugal). *Acta Oecologica* 23: 421 – 429.

Corriero, A., S. Desantis, M. Delflorio, F. Acone, C. R. Bridges, J. M. De Le Serna, P. Megalofonou and G. D. Metrio. 2003. Histological investigation on the ovarian cycle of the bluefin tuna in the western and central Mediterranean. *J. Fish Biol*., 63: 108 – 119.

Cortes, E. 1997. A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. *Can. J. Fish. Aquat. Sci*., 54: 726 – 738.

Costa, A. M. 2009. Macroscopic vs. microscopic identification of the maturity stages of female horse mackerel. *ICES J. Mar. Sci*., 66: 509 – 516.

Costello, M. J. 1990. Predator feeding strategy and prey importance: a new graphical analysis. *J. Fish Biol*., 36: 261 – 263.

Coward, K. and N.R. Bromage, 1998. Histological classification of oocyte growth and the dynamics of ovarian recrudescence in *Tilapia zilli*. *J. Fish. Biol*., 53: 285 – 302.

Culkin, F. and R. J. Morris. 1970. The fatty acids of some marine teleosts. *J. Fish Biol*., 2 (2): 107 – 112.

Cunjak, R. A. and G. Power. 1987. The feeding and energetic of stream-resident trout in winter. *J. Fish Biol*., 31: 493 – 511.

Dorner, H., S.Berg, L. Jacobsen, S. Hulsmann, M. Brojerg and A. Wagner. 2003. The feeding behavior of large perch *Perca fluviatilis* (L.) in relation to food availability: A comparative study. *Hydrobiologia*, 506 (1): 427 – 434.

Darriba, S, F. S. Juan and A. Guerra.2005. Energy storage and utilization in relation to the reproductive cycle in the razor clam *Ensis arcuatus* (Jeffreys, 1865). *ICES J. Mar. Sci.,* 62 : 886 – 896.

Davis, T. L. O. and G. J. West. 1993. Maturation, reproductive seasonality, fecundity and spawning frequency in *Lutjanus vittus* (Quoy and Gaimard) from the northwest shelf of Australia. *Fish. Bull*., 91: 224 – 236.

de Crespin, Billy, V., S. Doldec and D. Chessel. 2000. Biplot presentation of diet composition data: an alternative for fish stomach analysis. *J. Fish. Biol*., 56 (4): 961 – 973.

de Jong, T. K. 1940. A preliminary investigation on the spawning habits of some fishes of Java Sea. *Treubia*, 17: 307 –327.

de Martini, E. E. and R. K. Fountain. 1981. Ovarian cycling frequency and batch fecundity in the queenfish *Seriphus politus* : attributes reperesentative of serial spawning fishes. *Fish. Bull*., 79: 547 -560.

de Martini, E. E., J. H. Uchiyama, H. A. Williams.2000. Sexual maturity, sex ratio and size composition of swordfish, *Xiphias gladius*, caught by Hawaii-based pelagic long line fishery. *Fish. Bull*., 98: 489 – 506.

de Silva, S. S., R. M. Gunasekera, R. Collins, B. A. Ingram and C. M. Austin. 1997. Changes in the fatty acid profile of the Australian short fin eel in relation to development. *J. Fish. Biol.*, 50 : 992-998.

de Vlaming,V. 1983. Oocyte development patterns and hormonal involvements among teleosts. *In*: Rankin, J .C., T. J. Pitcher, R. T.Duggan (Eds.) *Control Processess in Fish Physiology*, Croom Helm, London, p. 176 – 199.

de Vlaming,V., G.Grossman and F.Chapmen. 1982. On the use of gonosomatic index. *Comp. Biochem. Physiol*., 73A: 31 – 39.

Devanesan, D. W. and V. John 1940. On the natural history of *Rastrelliger kanagurta* (Russel) with special reference to its spawning season and eggs. *Curr. Sci*., **9**(10) : 462-64.

Devadoss, P. 1969. Maturity and spawning in *Otolithus ruber* (Schn.) and *Johnius dussumieri* (C. & V.). *Indian J. Fish*., 16: 117 – 128.

Devaraj, M. 1983. Maturity, spawning and fecundity of the king seer *Scomberomorus commerson* (Lacepede) in the seas around the Indian peninsula. *Indian J. Fish*., 30(2): 203 – 230.

Devaraj, M. 1999. Food and feeding habits of the king seer *Scomberomorus commerson* (Lacepede) in the seas around the Indian Peninsula. *J. Mar. Biol. Ass. India*,40: 69 90.

Devaraj, M., I. Fernandes and S. S. Kamat. 1994. Dynamics of the exploited Indian mackerel *Rastrelliger kanagurta* stock along the south-west coast of India. *J. Mar. Biol. Ass. India*, 36 (1&2): 110 – 151.

Devaraj, M., K.. N. Kurup, N.G.K. Pillai, K.Balan, E.Vivekanandan and R.Sathiadas. 1997. Status, prospects and management of small pelagic fisheries in India. *In*: Devaraj,M. and P. Martosubroto (Eds.) *Small Pelagic Resources and their Fisheries in the Asia-Pacific region*. Proc., APFIC Working Party on Marine Fisheries, Bangkok, Thailand, RAP Publn., 1997/ 31: 91 – 197.

Dharmamba, M. 1959. Studies on the maturation and spawning habits of some common clupeids of Lawson's Bay, Waltair. *Indian J. Fish*.,6 (2): 374 – 388.

Dhulkhed, M.H. 1968. Sex ratio and maturity stages of the oil sardine *Sardinella longiceps* Val. From the Mangalore zone. *Indian J. Fish*., 15: 116 – 126.

Dominguez-Petit, R. and Saborido-Rey, F. 2009. New bioenergetic perspective of European hake (*Merluccius merluccius* L.) reproductive ecology. *Fish. Res*., doi:10. 1016/j.fishres.2009.09.002

Dunstan, G. A., A. J. Sinclair, K. O'Dea and J.M. Naughton. 1988. The lipid content and fatty acid composition of various marine species from Southern Australian coastal waters. *Comp. Biochem Physiol*., 91B: 165 -169.

Durbin, E. G., A. G. Durbin, R.W. Langton and R. E. Bowman. 1983. Stomach contents of silver hake, *Merluccius bilinearis* and Atlantic cod *Gadus morhua*, and estimation of their daily rations. *Fish. Bul*l., 81: 437 – 454.

Edirsinghe, E. M. R. K. B., W. M. K. Perera and A.Bamunurachhi. 1998. Fatty acid composition of some small pelagic fishes in Sri Lanka. *Proc. Symp. Fish Utilisation in Asia and Pacific*. APFIC-RAP Publn., pp. 172 – 178.

Eenennaam , V. J. P. and S. I. Doroshov. 1998. Effects of age and body size on gonadal development of Atlantic sturgeon. *J .Fish Biol*., 53: 624 – 637.

Ellis, J.K. and J.A. Musick. 2007. Ontogenetic changes in the diet of the sandbar shark, *Carcharhinus plumbeus*, in lower Chesapeake Bay and Virginia (USA) coastal waters. *Environ. Biol. Fish*., 80: 51 – 67.

Engelhard, G. H. and M. Heino. 2004. Maturity changes in Norwegian spring-spawning herring before, during and after a major population collapse*. Fish. Res*., 66: 299 – 310.

Ernande, B. 2008. Fisheries-induced evolution of maturation schedule in exploited stocks: Emperical and theoretical evidence, expected demographic implications and potential mitigation measures. *Comp. Biochem. Physiol*., Part A, 150 (3): 205.

Exler, J., Kensella, J. E. and B. K. Watt. 1975. Lipids and fatty acids of important finfish: new data for nutrient tables. *J. Am. Oil Chem. Soc*., 52: 154 – 159.

Exler, J. and J.I. Weihrauch. 1976. # Comprehensive evaluation of fatty acids in foods. *J. Am. Diet. Assoc.*, 69; 243 – 248.

Farkas, T., I. Csengeri, F. Majoros and J. Olah. 1980. Metabolism of fatty acids of fish. III. Combined effect of environmental temperature and diet on formation and deposition of fatty acids in the carp. *Aquaculture*, 20 : 29 – 40.

Farkas, T., E .Fodor, K. Kitajka and J. E. Halver. 2001. Response of fish membranes to environmental temperature. *Aqua. Res.,* 32: 645 – 655.

Ferreri, R., G. Basilone, M. D'Elia, A. Traina, F. Saborido-Rey and S. Mazzola. 2009. Validation of macroscopic maturity stages according to microscopic histological examination for European anchovy. *Mar. Ecol*., 30(1): 181 – 187.

Figueiredo, M., T. Morato, J. P .Barreiros, P .Alfonso and R. S. Santos. 2005. Feeding ecology of the white sea bream *Diplodus sargus* and the ballan wrasse *Labrus bergylia* in the Azores. *Fish. Res*., 75: 107 – 119.

Finucane, J. H., L. A. Collins, H. A .Brusher and C. H. Soloman, 1986. Reproductive biology of king mackerel *Scomberomorus cavalla*, from the south eastern United States. *Fish. Bull*., 84(4): 841 – 850.

Flavia, M., T. V. Lucen, J. R. Ellis and C. M. O'Brien. 2000. Seasonal variation in the diets of bluefish *Pomatomus salatrix* (Pomatomidae) and striped weakfish *Cynoscion guatucupa* (sciaenidae) in southern Brazil: Implications of food partitioning. *Env. Biol. Fish*., 57 423 – 434.

Folch, J., M. Lees and Sloane-Stanley, G. H. 1957. A simple method for the isolation and purification of total lipids from animal tissues. *J. Biol. Chem*., 226: 497 – 509.

Forberg, K.G. 1982. A histological study of development of oocytes in capelin *Mallotus villosus* (Muller). *J.Fish Biol*., 20: 143 – 154.

Foucher, R. P. and R. J. Beamish. 1980. Production of non-viable oocytes of Pacific hake *Merluccius productus*. *Can. J. Fish. Aquat. Sci*., 37: 41 – 48.

Fritz, E.S. 1974. Total diet comparison in fishes by Spearman Rank Correlation Coefficient. *Copeia*, 1- 4: 210 – 214.

Froese, R. and D. Pauly (Eds.) 2010. FishBase, world Wide Web electronic publn., www.fishbase.org

Furuita, H., T. Takeuchi, T. Watanabe, H. Fujimota, S. Sekiya and K. Imaizumi. 1996. Requirement of larval yellowtail for eicosapentaenoic acid, docosahexaenoic acid and n-3 highly unsaturated fatty acid. *Fish. Sci*., 62: 372 – 379.

Funamoto, T., I. Aoki and Y. Wada. 2004. Reproductive characteristics of Japanese anchovy *Engraulis japonicus*, in two bays of Japan. *Fish. Res*., 70: 71 – 81.

Galap ,C., P .Netchitailo, F. Leboulenger and J. P. Grillot. 1999. Variations of fatty acid contents in selected tissue of female dog cockle (*Glycymeris glycymeris* L.) Mollusca Bivalvia) during the annual cycle. *Comp. Biochem. Physiol*., A. 122: 241 – 254.

Galarowicz, T. L., J. A. Adams and D. H. Wahl. 2006. The influence of prey availability on ontogenetic diet shifts of a juvenile piscivore. *Can. J. Fish. Aquat. Sci*., 63 (8): 1722 – 1733.

Gallagher, M. L., E. Kane and R. Beringer. 1984. Effect of size on composition of the American eel, *Anguilla rostrata*. *Comp. Biochem. Physiol*., 78A (3): 533 – 536.

Gallagher, M. L., S. H. McLeod, and R. Rulifson. 1989. Seasonal variations in fatty acids of Striped Bass *Morone saxitilis*. *J. World Aquaculture Society*, 20(2):38 – 45.

Garrison, L. P. and J. S. Link. 2000. Dietary guild structure of the fish community in the northeast United States continental shelf ecosystem. *Mar. Ecol. Prog. Ser*., 202: 231 – 240.

Gascuel, D., Y-M . Bozec, E. Chassot, A. Colomb and M .Laurans. 2005. The trophic spectrum: theory and application as an ecosystem indicator. *ICES J. Mar. Sci*., 62: 443 – 452.

Gatten, R. R., J. R. Sargent and J. C. Gamble. 1983. Diet-induced changes in fatty acid composition of herring larvae reared in enclosed ecosystems. *J. Mar. Biol. Ass. U.K*., 63: 575 – 584.

Gerritsen, H.D. and D.McGrath. 2006. Variability in the assignment of maturity stages of plaice *Pleuronectes platessa* L. and whiting (*Merlangius merlangus* L.) using macroscopic maturity criteria. *Fish. Res*., 77: 72 – 77.

Gnanamuttu, J. C. 1971. On the occurrence of *Rastrelliger faughni* Matsui in the Indian waters. *Indian J. Fish*., 18 (1 &2): 170 - 173.

Gnaiger, E. and G. Bitterlich.1984. Proximate biochemical composition and caloric content calculated from elemental CHN analysis: a stoichiometric concept. *Oecologia* (Berlin), 62: 289 -298.

Goncalves, E. J. and V. C. Almada. 1997.Sex differences in resource utilization by the Peacock blenny. *J. Fish Biol*., 51: 624 – 633.

Gopakumar, G. , N. Gopalakrishna Pillai and T. A. Omana 1991. The fishery characteristics and biology of mackerel at Vizhinjam. *J. mar. biol. Ass. India*, 33 (1&2) : 107-114.

Gopakumar, K. 1969. Seasonal variation in lipid composition of oil sardine *Sardinella longiceps*. *Indian J. Fish*., XII (1), 1-5.

Gopakumar, K. (Ed.). 1993. *Biochemical composition of Indian food fish.* Central Institute of Fisheries Technology, 44p.

Gopakumar, K. and Nair, R. M. 1971. Phospholipids of five Indian food fishes. *Fish. Technol*., 8(2): 171 – 173.

Gopinathan, C.P., P. V. R. Nair and A. K. V, Nair. 1984. Quantitative ecology of phytoplankton in the Cochin backwater. *Ind. J. Fish*., 325 – 336.

Goekce, M. A., O. Tasbozan, M. Celik and S. S. Tabakoglu. 2004. Seasonal variations in proximate and fatty acid compositions of female common sole (*Solea solea*). *Food Chem*., 88: 419 – 423.

Goetz, F.W. 1983. Hormonal control of final oocyte maturation and ovulation in fishes. *In*: W.S. Hoar, D. J. Randall and E. M. Donaldson (Eds.) *Fish Physiology* Vol. IX (B) *Reproduction*, Academic Press, pp. 117 – 170.

Gooch, J.A., M. B. Hale, T. Brown, Jr., J.C. Bonnet, C. G. Brand and L. W. Regier. 1987. Proximate and fatty acid composition of forty southeastern U.S. finfish species. *NOAA Technical Report NMFS,* 54. U.S.Dept. of Commerce.

Gordo, L.S., A. Costa, P. Abaunza, P. Lucio, A.T.G.W. Eltnik and I. Figueiredo. 2008. Determinate versus indeterminate fecundity in horse mackerel. *Fish. Res*., 89: 181 – 185.

Gopalakrishnan, A. 1991. Studies on some aspects of the reproductive physiology of the female grey mullet, *Mugil cephalus* (L.).Ph.D thesis, Cochin University of Science and Technology, Cochin, 214 p.

Graham, B. S., D. Grubbs, K. Holland and B. N. Popp. 2007. A rapid ontogenetic shift in the diet of juvenile yellowfin tuna from Hawaii. *Mar. Biol*., doi.10.1007/soo227-006-0360-y.

Gruger, E. H. Jr., R. W. Nelson and M. E. Stansby.1964. Fatty acid composition of oils from 21 species of marine fish, freshwater fish and shellfish. *J. Am. Oil Chemists Soc*., 41 : 662 – 667.

Graeve, M., G. Kattner and W. Hagen. 1994. Diet induced changes in the fatty acid composition of Arctic herbivorous copepods - Experimental evidence of trophic markers. *J. Exp. Mar. Biol. Ecol*., 182: 97 – 110.

Greer walker, M., P. R. Witthames and B. I, Santos.1994. Is the fecundity of the atlantic mackerel (*Scomber scombrus* : Scombridae) determinate? *Sarsia*, 79: 13 – 26.

Griffiths, S. P., G. C. Fry, F. J. Manson and R. D. Pillans. 2007. Feeding dynamics, consumption rates and daily ration of longtail tuna *Thunnus tonggol* in Australian waters, with emphasis on the consumption of commercially important prawn*. Mar. Freshw. Res*., 58: 376 – 397.

Griffiths, S. P., P. M. Kunhert, G. F. Fry and F. J. Manson. 2009. Temporal and size-related variation in the diet, consumption rate, and daily ration of mackerel tuna (*Euthynnus affinis*) in neretic waters of eastern Australia. *ICES J. Mar. Sci*., 66: 720 – 733.

Gunasekera, R .M., S. S. De Silva and B. A. Ingram. 1999. Early ontogeny related changes of the fatty acid composition in the percichthyid fishes trout cod, *Maculochella macquarensis* and Murray cod *Macullochella peelii peelii*. *J. Aquat. Living Resources*., 12: 219 – 227.

Guraya, S.S. 1993. Follicular (or oocyte) atresia and its causes and functional significance in the fish ovary. *In:* B.R. Singh (Ed.) *Advances in Fish Research*, Vol.1 pp. 313 – 332.

Hanson, J. M. and G. A. Chouinard. 2002. Diet of Atlantic cod in the southern Gulf of St. Lawrence as an index of ecosystem change, 1959 – 2000. *J. Fish Biol*., 60: 902 – 922

Hansson, S. 1998. Methods of studying fish feeding: a comment. *Can. J. Fish. Aquat. Sci.,* 55: 2706 – 2707.

Halilogulu,H. I., A. Bayir, A. N. Sirkecioglu, N. M. Aras and M. Atamanalp. 2004. Comparison of fatty acid composition in some tissues of rainbow trout (*Oncorhynchus mykiss*) living in seawater and freshwater. *Food Chemistry*, 86(1): 55 -59.

Hardy, M. and P. Mackie. 1969. Seasonal variation in some of the lipid components of sprats (*Sprattus sprattus*) . *J. Sci. Food Agric*. 20: 193 – 198.

Hardy, R. and Keay, J. N. 1972. Seasonal variations in the chemical composition of Cornish mackerel *Scomber scombrus* L., with detailed reference to lipids*. J. Food Technol.*, 7(2): 125 –137.

Hasek, B. E. and D. L. Felder. 2006. Biochemical contents of the ovary and hepatopancreas of *Uca longisignalis* and *Uca.nr.minax*. *Scienta Marina*, 70 (3): 505 – 517.

Hay, D. E., and J. R. Brett. 1988. Maturation and fecundity of Pacific herring (*Clupea harengus pallasi*): an experimental study with comparisons to natural populations. *Can. J. Fish . Aquat. Sci*., 45: 399 – 406.

Hayashi, K. and T. Takagi. 1977. Seasonal variations in lipids and fatty acids of sardine (*Sardinops melanosticta*). *Bull. Fac. Fish. Hokkaido Univ*. 28(2): 83 -94.

Hayashi, K. and T.Takagi. 1978. Seasonal variations in lipids and fatty acids of Japanese anchovy, *Engraulis japonica*. *Bull. Fac. Fish. Hokkaido Univ*., 29: 38 – 47.

Hazra, A. K., S. Ghosh, S. Banerjee and B. Mukherjee. 1998. Studies on lipid and fatty acid compositions of puffer livers from Indian coastal waters with seasonal variation. *J. Am. Oil Chem. Soc*., 75: 1673 - 1678.

Healey, M.C. and W.R. Heard. 1984. Inter and intra population variation in the fecundity of Chinook salmon (*Oncorhynchus tshawytsch*) and its relevance to life history theory. *Can. J. Fish. Aquat. Sci*., 41 (3): 476 – 483.

Helser, T. E., and F. P. Almeida. 1997. Density – dependant growth and sexual maturity of silver hake in the north-east Atlantic. *J. Fish Biol*., 51: 607 – 623.

Henderson, R. J. and S. M. Almatar. 1989. Seasonal changes in the lipid composition of herring (*Clupea harengus*) in relation to gonad maturation. *J. Mar. Biol. Ass. U.K*., 69: 323 – 334.

Henderson, R. J., M. V. Bell and J. R. Sargent. 1985. Bio-conversion of polyunsaturated fatty acids to prostaglandins by tissue homogenates of the turbot *Scopthalmus maximus* (L.). *J. Exp. Mar. Biol. Ecol*., 85: 93 – 99.

Henderson, R. J., J. R. Sargent and C. C. E. Hopkins. 1984. Changes in the content and fatty acid composition of lipid in an isolated population of the capelin during sexual maturation and spawning. *Mar. Biol*, 78: 255 –263.

Henderson, R. J., J. R. Sargent and B. J. S. Pirie. 1984a. Fatty acid catabolism in the capelin *Mallotus villosus* (Mueller) during sexual maturation. *Mar. Biol. Lett*. 5 : 115 – 126.

Henderson, B. A., J. L. Wong and S. J. Nepszy. 1996. Reproduction of walleye in Lake Erie: Allocation of energy. *Can. J. Fish. Aquat. Sci*., 53: 127 – 133.

Hesselsein, R. H., K. A. Hollard and P. Ramlal. 1993.Replacement of sulfur, carbon and nitrogen in tissue of growing broad whitefish (*Coregonus nasus*) in response to change in diet traced byΩ34S, 13 C and 15 N. *Can. J. Fish. Aquat. Sci*., 50: 2071 – 2076.

Henderson, B. A. and J. L. Wong. 1998. Control of lake trout reproduction- role of lipids. *J. Fish Biol*., 52: 1078 – 1082.

Hilborn, R and C. J. Walters. 1992. *Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertanity*. Kluwer Academic, London, 570 p.

Hislop, J. R. G., A . P. Robb and J. A. Gauld 1978. Observations on the effects of feeding level on growth and reproduction in the haddock, *Melanogrammus aeglefinus* (L.) in captivity. *J. Fish Biol.,*, 13 : 85-98.

Holden, M. J. and D. F. S. Raitt. 1974. Manual of Fisheries Science. 2. Methods of Resource investigation and their application. *FAO Fisheries Technical Paper* no. 115, rev. 1, 211p.

Holt, S. J. 1959. Report of the International training Centre on the Methodology and Techniques of Research on mackerel (*Rastrelliger*). Report No. 1095, FAO, Rome.

Hovde, S. C., O. T. Albert and E. M. Nilssen. 2002. Spatial, seasonal and ontogenetic variation in diet of northeast Arctic Greenland halibut (*Reinhardtius hippoglossoides*). *ICES J. Mar. Sci*., 59: 421 – 437.

Hunter, J. R. and S. R. Goldberg 1980. Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax. Fish. Bull*., 77: 641 – 652.

Hunter, J. R and R .J. H. Leong. 1981. Spawning energetics of female northern anchovy *Engraulis mordax*. *Fish. Bull*., 79: 215 – 230.

Hunter, J. R , N. C. H. Lo and R. J. H. Leong. 1985. Batch fecundity in multiple spawning fishes. In: Lasker,R. (Ed.). An egg production method in estimating spawning biomass of pelagic fish: Application to the northern anchovy, *Engraulis mordax*. *NOAA Tech. Rep., NMFS* 36, 67 - 78.

Hunter, J. R, B. J. Macewicz, C. H. Lo and C. A. Kimbrell. 1992. Fecundity, spawning and maturity of female Dover sole, *Microstomus pacificus*, with an evaluation of assumptions and precision. *Fish. Bull*., 90(1): 101 – 128.

Hunter, J. R. and B. J. Macewicz 1985. Rates of atresia in the ovary of captive and wild northern anchovy, *Engraulis mordax*. *Fish. Bull*., **83** : 119-136.

Hunter, J. R. and B. J. Macewicz 1985a. Measurement of spawning frequency in multiple spawning fishes. *NOAA Tech. Rep., NMFS* 36, 79 - 94.

Hyslop, E.J. 1980. Stomach content analysis – a review of methods and their application. *J. Fish Biol*., 17: 411 –429.

Hynes, H. B. N. 1950 The food of fresh-water sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*) , with a review of methods used in the studies of the food of fishes. *J. Anim. Ecol*., 19: 36 – 58.

Ikeda, T. 1996. Metabolism, body composition and energy budget of the mesopelagic fish *Maurolicus muelleri* in the sea of Japan. *Fish. Bull*., 94 (1): 49 – 58.

Iles, T. D. 1974. The tactics and strategy of growth in fishes. *In*: F.R.Harden Jones (Ed.), *Sea Fisheries Research*, John Wiley and Sons, New York, pp. 331 – 345.

Ishihara, K. and H. Saito. 1996. The docosahexaenoic acid content of the lipid of juvenile bluefin tuna *Thunnus thynnus* caught in the sea off Japanese coast. *Fish. Sci*., 62 : 840 – 841.

Iverson, S. J., K. J. Frost and S. L. C. Lang. 2002. Fat content and fatty acid composition of forage fish and invertebrates in Prince William Sound, Alaska: Factors contributing to among and within species variability. *Marine ecology Progress Series* 241: 161 –181.

Iverson, S. J., K.J. Frost and L. L. Lowry. 1997. Fatty acid signatures reveal fine structure of foraging distribution of harbor seals and their prey in Prince William Sound, Alaska. *Marine ecology Progress Series* 151: 225 – 271.

Izquierdo, M. S., H. F. Palacios and A. G. J. Tacon. 2001. Effect of broodstock nutrition on reproductive performance of fish. *Aquaculture*, 197: 25 – 42.

Jacob, P. G. and M. D. Rajagopal. 1980. Variations in stomach contents and biochemical composition of tissues in some marine fishes. *Ind. J. Mar. Sci*., 9: 207 – 211.

James, P. S. B. R. and M. Badrudeen. 1986. Studies on maturation and spawning of the fishes of the family Leiognathidae from the seas around India. *Indian J. Fish.,* 33 (1): 1 – 26.

James, P. S. B. R. and V. M. Baragi, 1980. The ovary as an indicator of frequency of spawning in fishes. *Proc. Indian Natl. Sci. Acad*., 46B (4): 479 – 489.

James, P. S. B. R. and C.Vasudevappa, 1978. Studies on maturity and spawning of the marine catfish *Tachysurus dussumieri* (Valenciennes) along the south Kanara coast. *Proc. Indian Natl. Sci. Acad*., 46 (1): 90 – 95.

Jensen, A. J. 1980. The 'Gut Index' a new parameter to measure the gross nutritional state of arctic charr *Salvelinus alpinus* (L) and brown trout *Salmo trutta* (L). *J. Fish Biol*., 17: 741 -747

Jenkins, G. P., N. E. Milward and R. F. Hartwick. 1984. Food of larvae of Spanish mackerels , genus *Scomberomorus* (Teleostei: Scombridae) in shelf waters of the great Barrier Reef. *Mar. Freshw. Res*., 35 (4): 477 – 482.

Jennings, S., M. J. Kaiser and J. D. Reynolds.2001. *Marine Fisheries Ecology*. Blackwell Science, Oxford.

Jayasankar, P. and K. Dharmalingam. 1997. Analysis of RAPD polymorphisms in *Rastrelliger kanagurta* off India. *Naga, the ICLARM Quarterly* (July- December), 52 – 56.

Jeziereka, B., Hazel, J. R. and S. D. Gerking. 1982. Lipid mobilization during starvation in the rainbow trout, *Salmo gairdneri* Richardson, with attention to fatty acids. *J. Fish Biol.*, 21: 681 – 692.

Johannes, R. E. 1978. Reproductive strategies of coastal marine fishes in the tropics. *Env. Biol. Fish.*, 3: 65 –84.

Johnson, R. B. 2009. Lipid deposition in oocytes of teleost fish during secondary oocyte growth. *Reviews in Fisheries Science*, 17(1): 78 – 89.

Jones S. and E. G. Silas. 1962. Mackerel from the Andaman sea. *Proc. Symp.Scomb.Fish*., Part 1: 255 – 282.

Jong Ju Se, J. R. Kucklick, T. Kozlova and H. R. Harvey 1997. Lipid accumulation and fatty acid composition during maturation of three pelagic fish species in lake Baikal. *J. Great Lakes Res.* **23**(3): 241-53.

Jonnson, N., B.Jonsson and L.P. Hansen. 1991. Energetic cost of spawning in male and female Atlantic salmon (*Salmo salar* L). *J. Fish. Biol*., 39 : 739 – 744.

Jorgensen, T. 1990. Long-term changes in age at sexual maturity of northeast Arctic cod (*Gadus morhua* L.). *J.Cons.Perm.Inter. Explor. Mer*., 46: 235 – 248.

Jorgensen, E. H., S. J. S.Johansen and M. J. Jobling. 1997. Seasonal patterns of growth, lipid deposition and lipid depletion in anadromous Arctic charr. *J. Fish Biol.,* 51: 312 –326.

Joseph, J. 1963. Fecundity of yellowfin tuna (*Thunnus albacares*) and skipjack (*Katsuwonus pelamis*) from the eastern pacific ocean. *Inter-American Tropical Tuna Commission Bulletin*, 7: 255 – 292.

June, F. C. 1953. Spawning of yellowfin tuna in Hawaiian waters. *Fish. Bull*., 54: 47 – 64.

Junquera, S., E. Roman, X. Paz and G. Ramilo. 2004. Changes in Greenland Halibut growth, condition and fecundity in the northwest Atlantic (Flemish Pass, Flemish cap and Southern Grand Bank). *J. Northw. Atl. Fish. Sci*., 25 : 17 – 28.

Kagwade, V. N. 1968. Maturation and spawning of the horse-mackerel *Caranx kalla* Cuv. and Val.. *Indian J. Fish*., 15: 207 – 220.

Kagwade, V. N. 1970. Maturation and spawning in *Polynemus heptadactylus* Cuv. and Val.. *Indian J. Fish*., 17: 76 – 89.

Kamler, E. 2005. Parent-egg-progeny relationships in teleost fishes: An energetic perspective. *Rev. Fish Biol. Fish*., 15: 399 – 421.

Kamler, E. 1992. *Early Life History of Fish: An Energetics Approach*. Fish and Fisheries Series 4, Chapman and Hall, London, 267 p.

Kanazawa,A., S.I.Teshima and K.Ono. 1979. Relationship between essential fatty acid requirements of aquatic animals and the capacity for bioconversion of linolenic acid to highly unsaturated fatty acids. *Comp. Biochem. Physiol*., 63B: 295 – 298.

Kaneko, T., M.Takeuchi, S.Ishii., H.Hideo andT. Kikuchi. 1966. Effect of dietary lipids on fish under cultivation –IV. Changes of fatty acid composition in flesh lipids of rainbow trout on non-feeding. *Bull. Jap. Soc. Fish*., 33 : 56 – 58.

Kapoor , B.G., H. Smith and I. A. Verighina. 1975. The alimentary canal and digestion in teleosts. *Advances in Marine Biology*, 13: 109 – 239.

Kas'yanov, S. P, T.A. Sayapina, G.M. Gor'kavaya, E.A. Naumenko and V.N. Akulin. 2002. Correlation between the lipid composition of the Anadyr capelin *Mallotus villosus* and its physiological state. *J. Evolutionary Biochemistry and Physiology*, 38(1): 65 -71.

Kathirvelu, P.S., P. Brown, D.Stoessel and A.Giles. 2003. Maturation and reproductive biology of the female wild carp *Cyprinus carpio* in Victoria, Australia. *Env. Biol. Fish*., 68: 321 – 332.

Katsukawa, T. 1997. Points of view Introduction of spawning potential: improvement in the threshold management theory. *Rev. Fish Biol. Fish*., 7: 285 – 289.

Kawakami, T. and K. Tachihara. 2005. Diet shift of juvenile and landlocked Ryuku-ayu *Plecoglossus altivelis ryukyuensis* in the Fukuji Reservoir, Okinawa Island, Japan. *Fish. Sci*., 71: 1003 – 1009.

Keast, A. and J.M.A. Eadie. 1985. Growth depensation in the year 0 large mouth Bass- the influence of diet. *Trans. Am. Fish Soc*., 114 : 204 – 213.

Kharlamenko,V. I., N.V. Zukhova, S. Khotimechenko, V.I. Svetachev and G. M. Kameneve. 1995. Fatty acids as markers of food sources in a shallow water hydrothermal ecosystem, (Kraternaya Bight, Yankich Island, Kurile islands.). *Mar. Ecol. Prog. Ser*., 120 : 231 –241.

King, M. 1995. *Fisheries Biology, Assessment and Management*. Fishing News Books, Oxford.

Kinsella, J.E., J. L. Shimp, J. Mai and J. Weihrauch. 1977 Fatty acid content and composition of freshwater finfish. *J. Am. Oil Chem. Soc*., 54: 424 -429.

Kirsch, P. E., S. J. Iverson, W. D. Bowen, S. R. Kerr and R. G. Ackman. 1998. Dietary effects on the fatty acid signature of whole Atlantic cod (*Gadus morhua*) *Can. J. Fish. Aquat. Sci*., 55:1378 -1386.

Kjesbu, O. S. 1994. Time of start of spawning in Atlantic cod (*Gadus morhua*) in relation to vitellogenic oocyte diameter, temperature, fish length and condition. *J. Fish Biol*., 45: 719 – 735.

Kjesbu, O. S., J. Klungsoyr, H. Kyrvi, P. R. Witthames and M. G. Walker 1991. Fecundity, atresia and egg size of captive atlantic cod (*Gadus morhua*) in relation to proximate body composition. *Can. J. Fish. Aquat. Sci*., **48**(12) : 2333-43.

Kjesbu, O. S., H. Kryvi and B. Norberg. 1996 a. Oocyte size and structure in relation to plasma steroid hormones in individually monitored, spawning Atlantic cod. *J. Fish Biol*., 49: 1197 – 1215.

Kjesbu, O. S., P. Solemdal, P. bratland and M. Fonn. 1996. Variation in annual egg production in individual captive Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci,* 53 : 610 -620.

Kjesbu, O. S., P. R. Witthames, P. Solemdal and M. Greer Walker. 1998. Temporal variations in the fecundity of arcto-Norwegian cod (*Gadus morhua*) in response to natural changes in food and temperature . *J. Sea Res*., 40: 303 – 321.

Knipprath, W. G. and J. F. Mead. 1966. Influence of temperature on fatty acid patterns of mosquito fish (*Gambusia afinis*) and guppies (*Lebistes reticulates*). *Lipids* 1:113 -117.

Knutsen, G. M. and S. Tilseth. 1985. Growth, development and feeding success of Atlantic cod *Gadus morhua* larvae related to egg size. *Trans. Am. Fish. Soc*., 114; 507 – 511.

Koslow, J. A. 1992. Fecundity and the stock-recruitment relationship. *Can. J. Fish. Aquat. Sci.,* 49: 210 – 217.

Koslow, J. A., J. Bell, P. Virtue and D. C. Smith. 1995. Fecundity and its variability in orange roughy: effects of population density, condition, egg size and senescence. *J. Fish. Biol*., 47: 1063 - 1080.

Kozlova, T. and S. Khotimchenko. 1993. Fatty acid composition of endemic Baikal fish and crustacea. *Comp. Biochem. Physiol*., 105B: 97 – 103.

Kraak, G. V. D., J. P. Chang and D. M. Janz. 1998. Reproduction. *In*: Evans, D. H. (Ed.) *The Physiology of Fish*, CRC Press, pp. 465 – 488.

Krishnamoorthi, B. 1971. Biology of the threadfin bream *Nemipterus japonicus* (Bloch). *Indian J. Fish*., 18 (1& 2): 1 – 21.

Krzynowek, J. and J. Murphy. 1987. Proximate composition, Energy, fatty acid, sodium and cholesterol content of finfish, shellfish and their products. *NOAA Technical Report NMFS* 55, 53 p.

Krzynowek, J., J. Murphy, R. S. Maney and L. J. Panunzio. 1989. Proximate composition and fatty acid and cholesterol content of 22 species of Northwest Atlantic finfish. *NOAA Technical Report NMFS* 74, 35 p.

Kulbicki, M., Y-M. Bozec, P. Labrosse, Y. Letourneur, G. Mou-Tham and L.Wantiez. 2005. Diet composition of carnivorous fishes from coral reef lagoons of New Caledonia. *Aquat. Living Resour*., 18: 231 – 250.

Kumaran, M. 1962. Studies on the food of *Euthynnus affinis affinis* (Cantor), *Auxis thazard* (Lacepede), *Auxis thynnoides* Bleeker and *Sarda orientalis* (Teminck and Schlegel). *Proc. Scomb. Fish*., part 2: 599 – 606.

Kutty, M. Narayanan. 1965. Observations on the Indian mackerel *Rastrelliger canagurta* (Cuvier) from the trawl catches along the Bombay coast. *Indian J. Fish*., 9A(2): 590 – 603.

Kuthalingam, M. D. K. 1956. Observations on the food and feeding habits of the Indian mackerel *Rastrelliger kanagurta* (Russell). *J. Zool. Soc. India*, 8: 99 – 106.

Labropoulou, M. , A. Machias, N. Tsimenides and A. Eleftheriou. 1997. Feeding habits and ontogenetic diet shift of the striped red mullet *Mullus surmuletus* Linnaeus, 1758. Fish. Res., 31: 257 – 267.

Lam, T. J. 1983. Environmental influences on gonadal activity in fish. *In*: W.S. Hoar, D. J. Randall and E. M. Donaldson (Eds.) *Fish Physiology* Vol. IX (B) *Reproduction*, Academic Press, pp. 65 – 116.

Lambert, T.C. 1990. The effect of population structure on recruitment in herring. *J. Cons. Int. Explor. Mer*., 47: 249 – 255.

Lambert, T. C. and D. M. Ware. 1984. Reproductive strategies of demersal and pelagic spawning fish. *Can. J. Fish. Aquat. Sci*., 41: 1565 – 1569.

Lambert, Y. 2008. Why should we closely monitor fecundity in marine fish populations. *J. Northw. Atl. Fish. Sci*., 41: 93 – 106.

Lambert, Y. and J. D. Dutil. 1998. Energetic consequences of reproduction in Atlantic cod (*Gadus morhua*) in relation to spawning level of somatic energy reserves. *Can. J. Fish. Aquat. Sci*., 57(4): 815 – 825.

Lambert, Y., J. D. Dutil and P. Ouellet. 2000. Nutritional condition and reproductive success in wild fish populations. *Reproductive Physiology of Fish, 6th International Symposium*, Bergen (Norway), 4-9 July, pp. 77 -84.

Langton, R.W. 1982. Diet overlap between Atlantic cod *Gadus morhua*, silver hake, *Merluccius bilinearis* and fifteen other Northwest Atlantic finfish. *Fish Bull.*, 80: 745 -759.

Lapitkhovsky,v.V., A.I.Arkhipkin, D.A.J.Middleton and L.R.Butcher. 2002. Ovary maturation and fecundity of the squid *Loligo gahi* on the south east shelf of Falkland islands. *Bull. Mar. Sci*., 71 (1): 449 -464.

Lasker, R. 1985. An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy *Engraulis mordax*. *U.S. Dept. Commer. NOAA Tech. Rep. NMFS 36.*

Lasker, R. and G. H. Theilacker. 1962. The fatty acid composition of the lipids of some Pacific sardine tissues in relation to ovarian maturation and diet. *J. Lipid Res*., 3: 60 – 64.

Lauth, R. R. and R. J. Olsen, 1996. Distribution and abundance of larval scombridae in relation to the physical environment in the northwestern Panama Bight. *Inter-Amer. Trop. Tuna Comm. Bull*., 21 (3): 127 – 167.

Lea, Mary-Ann., P.D.Nichols and G.Wilson. 2002. Fatty acid composition of lipid-rich myctophids and mackerel icefish (*Champsocephalus gunnari*) – Southern Ocean food-web implications. *Polar Biol*., 25 : 843 – 854

Lee, R. F., J. C. Nevenzel and G. A. Paffenhoffer. 1971. Importance of wax esters and other lipids in the marine food chain: phytoplankton and copepods. *Mar. Biol*., 9: 99 – 108.

Liao, H., C. L. Pierce and J. G. Larscheid. 2001. Empirical assessment of indices of prey importance in the diets of predacious fish. *Trans. Am. Fish. Soc*., 130: 583 – 591.

Lima, S.E. Jr. and R. Goitein, 2001. A new method for the analysis of fish stomach contents. *Acta Scientarum*, 23 (2): 421 – 424.

Link, J. S. and L. P. Garrison, 2002. Trophic ecology of Atlantic cod *Gadus morhua* on the northeast US Continental shelf. *Mar. Ecol. Prog. Ser*., 227: 109 – 123.

Linko , R., J. K. Kaitaranta and R. Vuorela. 1985. Comparison of the fatty acids in Baltic herring and available plankton feed. *Comp. Biochem. Physiol*., 82 B: 699 – 705.

Longhurst, A. R. and D. Pauly. 1987. *Ecology of Tropical Oceans*. Academic Press, London.

Lowe, C. G., B. M. Wetherbee, G. L. Crow and A. L. Tester. 1996. Ontogenetic dietary shifts and feeding behavior of the tiger shark *Galeocerdo cuvieri*, in Hawaiian waters. *Environ. Biol. Fish*., 47: 203 – 211.

Luther, G. 1973. Observations on the biology and fishery of the Indian mackerel *Rastrelliger kanagurta* (Cuvier) from Andaman islands. *Indian J. Fish*., 20(2): 425 – 447.

Macchi, G. J. 1998. Prliminary estimate of spawning frequency and batch fecundity of striped weak fish *Cynoscion striatus* in coastal waters off Buenos Aires Province. *Fish. Bull.,* 96 (2): 375 –381.

Macchi, G. J. and E. M. Acha. 2000. Spawning frequency and batch fecundity of Brazilian menhaden *Brevoortia aurea* in the Rio de la plata estuary off Argentina and Uruguay. *Fish. Bull.,* 98: 283 –289.

Macchi , G. J., P. Marcelo and M. Ehrlich. 2004. Seasonal egg production pattern of the Patagonian stock of Argentine hake (*Merluccius hubbsi*). *Fish. Res.*, 67: 25 -38.

Macdonald, J. S. and R. H. Green. 1983. Redundancy of variables used to describe importance of prey species in fish diets. *Can .J. Fish. Aquat. Sci.*, 40: 635 – 637.

Macer, C. T. 1974. The reproductive biology of the horse mackerel *Trachurus trachurus* (L.) in the North Sea and English Channel. *J. Fish Biol*., 6(4): 415 – 438.

MacFarlane, B. R., E. C. Norton and M. J. Bowers. 1992. Lipid dynamics in relation to the annual reproductive cycle in yellowtail rockfish (*Sebastes flavidus*) *Can .J. Fish. Aquat. Sci.*, 50: 371 – 401.

Madhupratap, M.1999. Free –living copepods of the Arabian Sea: Distribution and research perspectives. *Ind. J. Mar. Sci*., 28: 138 – 145.

Madhupratap, M., S. R. Shetye, K. N.. Nair and R. S. Nair. 1994. Oil sardine and Indian mackerel: Their fishery problems and coastal oceanography. *Curr. Sci*., **66** (5): 340-348.

Madhupratap, M., K. N. V. Nair, T. C. Gopalakrishnan, P . Haridas, K. K. C. Nair, P. Venugopal and M. Gauns. 2001. Arabian Sea oceanography and fisheries. *Curr. Sci*., 81(4): 355 – 361.

Mahe, K., R. Amara, T. Bryckaert, M. Kacher and J. M. Brylinski.. 2007. Ontogenetic and spatial variation in the diet of hake (*Merluccius merluccius*) in the Bay of Biscay and the Celtic Sea. *ICES J. Mar. Sci*., 64: 1210 – 1219.

Mann, K. H. 1988. Production and use of detritus in various freshwater, estuarine, and coastal marine ecosystems. *Limnol. Oceanogr.* 33 (4, part 2): 910 – 930.

Manooch, C. S., D. L. Mason and R. S. Nelson. 1985. Foods of little tunny, *Euthynnus alletteratus* collected along the southeastern and Gulf coasts of the United States. *Bull. Jap. Soc. Sci. Fish*., 51: 1207 – 1218.

Marichamy, R. 1970. Maturity and spawning of the anchovy *Thrissina baelama* (Forskal) from the Andaman Sea. *Indian J. Fish*., 17 (1&2): 179 – 182.

Marichamy, R. 1971. Maturity and spawning of the spotted herring *Herklotsichthys punctatus* (Ruppell) from the Andaman Sea. *Indian J. Fish*., 18 (1&2): 148 – 155.

Marteinsdottir, G. and A. Steinarsson. 1998. Maternal influence on the size and viability of Icelandic cod *Gadus morhua* eggs and larvae. *J. Fish. Biol*., 52: 1241 -1258.

Marteinsdottir, G. and K. Thorarinsson. 1998. Improving the stock-recruitment relationship in Icelandic cod (*Gadus morhua*) by including ahe diversity of spawners. *Can. J. fish. Aquat. Sci*., 55: 1372 – 1377.

Marteinsdottir, G. and G. A. Begg. 2002. Essential relationships incorporating the influence of age, size and condition on variables required for the estimation of reproductive potential in Atlantic cod *Gadus morhua*. *Mar. Ecol. Prog. Ser*., 235: 235 – 256.

Marshall, C. T., O. S. Kjesbu, N. A. Yarogina, P. Solemdal and O. Ultang. 1998. Is spawner biomass a sensitive measure of the reproductive and recruitment potential of north east Arctic cod. *Can. J. Fish. Aquat. Sci.*, 55: 1766 –1783.

Marshall, C. T., N. A. Yaragina, Y. Lambert and O. S. Kjesbu 1999. Total lipid energy as a proxy for total egg production by fish stocks. *Nature*, 402 : 288-290.

Marshall, S. and M. Elliott. 1997. A comparison of univariate and multivariate numerical and graphical techniques for determining inter and intra-specific feeding relationships in estuarine fish. *J. Fish Biol*., 51(3): 526 – 545.

Masuda, R. 2003. The critical role of docosahexaenoic acid in marine and terrestrial ecosystems: from bacteria to human behavior. In: H.I. Browman and A.B. Skiftesvik (Eds.) *The Big Fish Bang*. Institute of Marine Research, Bergen, Norway, pp. 249 – 256.

Masuda, R. 2009. Behavioural ontogeny of marine pelagic fishes with the implication for the sustainable management of fisheries resources*. Aqua. Biosci. Monogr*. (ABSM), 2 (2): 1 – 56. www.terrapub.co.jp/onlinemonographs/absm

Mathew, S., K. Ammu, Nair, P.G.V and K. Devadasan. 1999. Cholesterol content of Indian fish and shellfish. *Food chem*.., 66: 455 – 461.

Matsuyama, M., S. Adachi, Y. Nagahama, K. Maruyama and M. Matsuura. 1990. Diurnal rhythm of plasma steroid hormone levels in the Japanese whiting *Sillago japonica*, a daily spawning teleost. *Fish. Physiol. Biochem*, 8 : 329 – 338.

Matsuyama, M. T. Fukuda, S. Ikeura, Y. Nagahama and M. Matsuura. 1991. Annual reproductive cycle of the captive female Japanese sardine *Sardinops melanostictus*: relationship to ovarian development and plasma levels of gonadal steroid hormones. *Mar. Biol*., 108: 21 – 29.

Mayer, I., S. E. Shackley and J. S. Ryland. 1988. Aspects of the reproductive biology of the bass *Dicentrarchus labrax (*L) 1. An histological and histochemical study of oocyte development. *J.Fish. Biol*., 33: 609 –622.

Mayer, I., S. E. Shackley and P. R. Witthames. 1988. Aspects of the reproductive biology of the bass *Dicentrarchus labrax (*L) 2. Fecundity and pattern of oocyte development. *J.Fish. Biol*., 36: 141 – 148.

Mayzaud, P., P. Virtue and E. Albessard. 1999. Seasonal variations in the lipid and fatty acid composition of the euphausiid *Meganyctiphanes norvegica* from the Liguran Sea. *Mar. Ecol. Prog. Ser*., 186: 199 – 210.

McDermott, S. F., K. P. Maslenikov and D. R. Gunderson. 2007. Annual fecundity, batch fecundity and oocyte atresia of Atka mackerel (*Pleurogrammus monopterygius*) in Alaskan waters. *Fish. Bull*., 105: 19 – 29.

McDowall, R. M. and G. A. Eldon. 1997. Reproductive cycling and fecundity estimation in upland bully. *J. Fish Biol*., 51 (1): 164 – 171.

McElroy,W. D., B. M. Wetherbee C. S. Mostello, C.G.Lowe, G. L. Crow and R.C.Wass. 2006. Food habits and ontogenetic changes in the diet of the sandbar shark *Carcharhinus plumbeus*, in Hawaii. *Environ. Biol. Fish*., 76(1): 81 – 92.

McEvoy, L.A. and J. K. McEvoy 1992. Multiple spawning in several commercial fish species and its consequences for fisheries management, cultivation and experimentation. *J.Fish Biol*, 41(b): 125 – 136.

McKenzie, D.J., D. A. Higgs, B. S. Dosanjh, G. Deacon and D. J. Randall. 1998. Dietary fatty acid composition influences swimming performance in Atlantic salmon (*Salmo salar*) in seawater. *Fish Physiol. Biochem*., 19: 111 -112.

McPherson, E. and C. M. Duarte. 1991. Bathymetric trends in demersal fish size: is there a general relationship. *Mar.Ecol. Prog.Ser*., 71: 103 – 112.

McPherson, G. R. 1991. Reproductive biology of yellowfin tuna in the eastern Australian fishing zone, with special reference to the north-western Coral Sea. *Aust. J. Mar. Freshw. Res*., 42: 465 – 477.

Medina, A., F.J. Abascal, C.Megina and A.Garcia. 2002. Stereological assessment of the reproductive status of female northern bluefin tuna during migration to Mediterranean spawning grounds through the straits of Gibraltar. *J. Fish Biol*., 60: 203 – 217.

Medina, I., S.P.Aubourg and R.P.Martin. 1995. Composition of phospholipids of white muscle of six tuna species. *Lipids,* 30: 1127 – 1135.

Menon, N. N., A. N. Balchand and N. R. Menon. 2000. Hydrobiology of the Cochin backwater system- a review. *Hydrobiologia,* 430: 149 – 183.

Menzes, M.R., S. Naik and M. Martins. 1993. Genetic divergence in the Indian mackerel *Rastrelliger kanagurta* (Cuv.) from the coastal waters of peninsular India and the Andaman sea. *Ind. J. Fish*., 40: 135 – 141.

Metcalfe , L.D. , A. A. Schmitz and J. R. Pelka. 1966. Rapid preparation of fatty acid esters from lipids for gas chromatographic analysis. *Anal. Chem*., 38(3): 514. (check : 33: 363 – 364)

Meziane,T. and Tsuchiya, M. 2000. Fatty acids as tracers of organic matter in the sediment and food web of a mangrove/intertidal flat ecosystem, Okinawa, Japan. *Mar. Ecol. Prog. Ser.,* 200: 49 – 57.

Miller, P.J. 1984. The tokology of gobioid fishes. In: G.W.Potts and R.J.Wootton (Eds.). Fish Reproduction: Strategies and Tactics. London, Academic Press

Milton,D.A., S.J.M.Blaber and N.J.F. Rawlinson. 1994. Diet, prey selection and their energetic relationship to reproduction in the tropical herring *Herklotsichthys quadrimaculatus* in Kiribati, Central Pacific. *Mar. Ecol. Prog. Ser*., 103: 239 – 250.

Mittelbach, G.J. 2002. Fish foraging and habitat choice: A theoretical perspective. *In*: Hart, P.J.B. and J. D. Reynolds (Eds.) *Handbook on Fish Biology and Fisheries*, Blackwell Publishing, p.249 – 266.

Mohan, M.V. and T. M. Sankaran. 1988. Two new indices for stomach content analysis of fishes. *J. Fish Biol*., 33 : 289 –292., pp. 119 – 154.

Mohamed, K. S., P. U. Zacharia, C. Muthiah, K. P.Abdurahiman and T. H. Nayak. 2008. Ttrophic modeling of the Arabian sea ecosystem off Karnataka and simulation of fishery yields. *Bull. Cent. Mar.Fish.Res. Inst., 51, 140 pp.*

Monteiro, P. M.S., A.G. James, A.D. Sholto Douglas and J.G.Field. 1991. The C trophic position isotope spectrum as a tool to define and quantify carbon pathways in marine food web. *Mar. Ecol. Prog. Ser*., 78: 33 – 40

Moreno,T., J.J. Castro and J.Socorro. 2005. Reproductive biology of the sand smelt *Atherina presbyter* Cuvier, 1829 (Pisces: Atherinidae) in the central-east Atlantic. *Fish. Res*., 72: 125 – 131.

Morgan, M. J. 2004. The relationship between fish condition and the possibility of being mature in American plaice (*Hippoglossoides plattesoides*). *ICES J. Sea.Res*., 44: 55 – 64.

Morgan, M. J. 2008. Integrating reproductive biology into scientific advice for fisheries management. J. *Northw. Atl. Fish. Sci*., 41: 37 -51.

Morgan, M. J. and G.R. Lilly. 2006. The impact of condition on reproduction in Flemish Cap cod. *J. NorthW. Atl. Sci*., 37: 81 – 86.

Morgan, M. J., P.A. Shetton and J.Brattey. 2007. Age composition of the spawning stock does not always influence recruitment. *J. Northw. Atl. Fish. Sci*., 38: 1- 12.

Mostardo, E., D.Campo, L.Castirota, V.Esposito, M.P. Scarabello and F.Andaloro. 2007. Feeding habits of the bullet tuna *Auxis rochei* in the southern Tyrrhenian Sea. *J. Mar. Biol. Ass. U.K*., 87 (4): 1007 - 1012.

Mourente,G., C.Megina, and E. Diaz-Salvago. 2002. Lipids in female northern bluefin tuna (*Thunnus thynnus thynnus* L.) during sexual maturation. *Fish Physiology and Biochemistry*, 24: 351 -363.

Mukundan, M.K., A.G.Radhakrishnan, M.A. James and P.D. Antony. 1981. Comparative study of the nutrient content of fish and shellfish. *Fish.Technol*., 18: 129 – 132.

Murdoch W.J., T.R. Hansen and L.A. McPherson. 1993. # A review: role of eicosanoids in vertebrate ovulation. *Prostaglandins*: 46: 85 – 115.

Murty, A.V.S. and M. N. Vishnudatta. 1976. The seasonal distribution of some oceanographic parameters off south-west coast of India related to pelagic fisheries. *Indian J. Fish*., 23 (1&2): 97 – 104.

Murua, H., L. A. Motos and P. Lucio. 1998. Reproductive modality and batch fecundity of the European hake (*Merluccius merluccius* L.) in the Bay of Biscay. *CalCOFI Rep*., 39: 196 – 203.

Murua, H. and F.Saborido-Rey. 2003. Female reproductive strategies of marine fish species of the north Atlantic. *J. Northw. Atl. Fish. Sci*., 33: 23 – 31.

Murua, H., G.Kraus, F.S.Rey, P.R.Witthames, A.Thorsen and S. Junquera. 2003. Procedures to estimate fecundity of marine fish species in relation to their reproductive strategy. *J. Northw. Atl. Fish. Sci*., 33: 33- 54.

Mylonas, C.C., Y. Magnus, Y. Klebanov, A.Gissis and Y. Zohar. 1997a. Reproductive biology and endocrine regulation of final oocyte maturation in captive white bass. *J.Fish Biol.*, 51: 234 – 250.

Mylonas, C.C., Woods,L.C. and Y.Zohar. 1997a. Cyto-histological examination of post-vitellogenesis and final oocyte maturation in captive-reared striped bass *Morone saxitilis* Walbaum). *J.Fish Biol*., 50: 34 – 49.

Nagahama,Y. 2000. Gonadal steroid hormones: major regulators of gonadal sex differentiation and gametogenesis in fish. *In*: Norberg, B, Kjesbu, O.S., G.L.Taranger, E.Anderson and S.O.Stefansson (Eds.) *Proc. 6th International Symp. on Reproductive Physiology of Fish*, Bergen, Norway, pp. 211 - 222.

Nair, R.V., S. K. Banerji, K. V. Rao, G.Venkataraman, K.V. N. Rao and V. Balakrishnan. 1970. The Indian mackerel. *Bull. Cent. Mar. Fish. Res. Inst*., 24, 102 p.

Nair, Viswanathan P.G. and K.Gopakumar. 1978. Fatty acid compositions of 15 species of fish from tropical waters. *J. of Food Science*, 43: 1162 –1164.

Nair, Viswanathan P.G. and K.Gopakumar. 1984. Lipid and Fatty acid composition of fish and shell fish. *J. of Food Science*, 21: 389 – 392.

Nair, Viswanathan P.G., K. Gopakumar and M. Rajendranathan Nair. 1976. Lipid hydrolysis in mackerel (*Rastrelliger kanagurta*) during frozen storage*. Fish. Technol*., 13(2): 111 –114.

Narayana,Rao, K. V. 1964. Food of the Indian mackerel *Rastrelliger kanagurta* (Cuvier) taken by drift nets in the Arabian sea off Vizhinjam, South Kerala. *Indian J. Fish*., ix (1): 530 –541.

Natarajan, A. V. and A. G. Jhingran. 1962. Index of Preponderance - a method of grading the food elements in the stomach analysis of fishes. *Indian J. Fish*.,8: 54 – 59 (1961).

Nath, P., R. Sahu, Sk. Kabita and D. Bhattacharya. 2007. Vitellogenesis with special emphasis on Indian fishes. *Fish Physiol Biochem*., 33: 359 – 366.

Navas, J. M., M. Bruce, M. Thrush, B. M. Farndale, N. Bromage, S. Z. Zanuy, M. Carillo, J. G. Bell and J. Ramos. 1997. The impact of seasonal alternation in the lipid composition of broodstock diets on egg quality in the European sea bass. *J.Fish Biol.*, 51: 760 –773.

Newell. R.C. 1984. The biological role of detritus in the marine environment In: *Flows of Energy and materials in marine ecosystems: theory and practice*. NATO Conf. Ser. 4. Mar. Sci. V. 13. Plenum., 317 – 343.

Nikolskii, G.V. 1969. *Theory of Fish Population Dynamics as the biological background for rational exploitation and management of fishery resources*. Otlo koeltz Science Publishers, 323 p.

Nichols, P.D., D.W. Klumpp, R.B. Johns. 1986. Lipid components and utilization in consumers of a seagrass community: an indication of carbon source. *Comp. Biochem. Physiol*, B 83: 103 – 113.

Njinkoue, J-M., G. Barnathan , J. Miralles, E- M. Gaydou and A. Samb. 2002. Lipids and fatty acids in muscle, liver and skin of three edible fish from the Senegalese coast: *Sardinella maderensis*, *Sardinella aurita* and *Cephalopholis taeniops*. *Comp. Biochem. Physiol*., B131: 395 – 402.

Noble, A. 1962. The food and feeding habits of the Indian mackerel *Rastrelliger kanagurta* (Cuvier) at Karwar. *Ind. J. Fish*., 9A(2): 701 – 713.

Noble, A. 1974. Fishery and biology of the mackerel *Rastrelliger kanagurta* (Cuvier) at Cochin. *J. mar. Biol. Ass. India* 16 (3):816 -829.

Noble, A. and P. Geetha. 1992. The Indian mackerel *Rastrelliger kanagurta* (Cuvier) an annotated bibliography. *CMFRI spl. Publn*., No. 52, 126 p.

Noble, A., G. Gopakumar, N. G. K. Pillai, G. M. Kulkarni, K. N. Kurup, S. Reuben, M. Sivadas and T. M. Yohannan. 1992. Assessment of mackerel stock along the Indian coast. *Ind. J. Fish*., 39: 11 – 24.

Nomura, T., H. Ogata and M. Hata. 1973. Occurrence of prostagalndins in fish testis. *Tohoku J. Agric. Res*., 21: 138 – 144.

Nordgarden, U., B. E. Torstensen, L . Froyland, T. Hansen and G. I. Hemre. 2003. Seasonally changing metabolism in Atlantic salmon (*Salmo salar* L) II. B oxidation capacity and fatty acid composition in muscle tissues and plasma lipoproteins. *Aquaculture Nutrition*, 9(5): 295 –304.

Olsen, E.M., M.Heino, G.R. Lilly, M.J.Morgan, J.Bratty, B.Ernande and U.Dieckmann. 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature*, 428: 932 – 935.

Omori, M. O. and T. Ikeda. 1984. *Methods in Marine Zooplankton Ecology*. John Wiley & Sons Inc.

Osako, K., A.Yamaguchi, T.Kurokawa, K.Kuwahara, H.Saito and Y.Nozaki. 2003. Seasonal variation in docosahexaenoic acid content in horse mackerel caught in the east China Sea. *Fisheries Science*, 69: 589 – 596.

Osako, K., H. Saito, M.A. Hossain, K. Kuwahara and A. Okamoto. 2006. Docosahexaenoic acid levels in the lipids of spotted mackerel *Scomber australasicus*. *Lipids*, 41(7): 713 – 720.

Osako, K., H. Saito, M.A. Hossain, K. Kuwahara and A. Okamoto. 2006a. Year-round high arachidonic acid level in herbivorous rabbit fish *Siganus fuscescens* tissues *Lipids*, 41(5): 473 – 489.

Oskarsson, G. J., O. S. Kjesbu and A. Slotte. 2002. Predictions of realized fecundity and spawning time in Norwegian spring-spawning herring (*Clupea harengus*). *J. Sea Res*., 48: 59 – 79.

Osman, F., I. Jaswir, H. Khaza'ai, R. Hashim. 2007. Fatty acid profiles of finfish in Langkawi Island, Malaysia. *J. Oleo Sci*., 56 (3): 107 -113.

Osman, H., A.R. Suria and E. C. Law. 2001. Fatty acid composition and cholesterol content of selected marine fish in Malaysia waters. *Food Chem.*, 73(1): 55 -60.

Ota,T., T. Takagi and S. Kosaka. 1980. Changes in lipids of young and adult saury, *Cololabis saira*. *Mar. Ecol. Prog. Ser*., 3: 11 – 17.

Otsu, T. and R.N. Uchida. 1959. Sexual maturity and spawning of albacore in the Pacific Ocean. *Fish. Bull*., 59: 287 – 305.

Pankhurst , N. W. and A. M. Conroy. 1988. Endocrine changes during gonadal maturation and spawning in the orange roughy (*Hoplostethus atlanticus* Colett) a teleost from the midslope waters off New Zealand. *Gen. Comp. Endocrinol*, 70: 262 – 273.

Parrish, R. H., D. L. Mallicoate and R .A. Klingbeil. 1986. Age dependant fecundity, number of spawning per year, sex ratio and maturation stages in northern anchovy. *Fish. Bull*., 1986: 84: 503 – 517.

Pati, S. 1982. Studies on maturation, spawning and migration of silver pomfret *Pampus argenteus* (Euphrasen) from Bay of Bengal. *Indian J.Fish*., 27: 244 – 256.

Penczak, T. 1985. A method of estimating total food consumed by fish populations. *Hydrobiologia*, 123: 241 – 244.

Penczak, T., E.Kusto, D.Kryzawska, M.Molinski and E.Suszycka. 1984. Food consumption and energy transformations by fish populations in two small lowland rivers in Poland. *Hydrobiologia*, 108: 135 – 144.

Persson, L. 1983. Food consumption and the significance of detritus and algae to intraspecific competition in roach *Rutilus rutilus* in a shallow eutrophic lake. *Oikos,* 4: 118 -125.

Persson, A. and C. Bronmark. 2002. Foraging capacity and resource synchronization in an ontogenetic diet switcher, Pike perch (*Stizostedion lucioperca*). *Ecology*, 83 (11): 3014 – 3022.

Peters, D. S. and M. A. Kjelson. 1975. Consumption and utilization of food by various post-larval and juvenile North Carolina estuarine fish. *In*: Cronin,L.E. (ed.) *Estuarine Research*, Vol.1, Academic Press, New York, USA.

Peters, D. S. and W. E. Schaff. 1981. Food requirements and sources for juvenile Atlantic menhaden. *Trans. Am. Fish. Soc*., 110: 317 – 324.

Peter, R.E. and K. L Yu. 1997. Neuroendocrine regulation of ovulation in fishes: basic and applied aspects. *Rev. Fish Biol. Fish*., 7: 173 – 197.

Phillips, K. L., G. D. Jackson and P. D. Nichols. 2003. Temporal variations in the diet of the squid *Moroteuthis ingens* at Macquarie Island: stomach contents and fatty acid analyses. *Mar. Ecol. Prog. Ser*., 256: 135 – 149.

Pillai, N.G.K., A.A. Jayaprakash and U.Ganga.2007. Status and scope of research on pelagic fisheries of India. *In*: M.J.Modayil and N.G.K. Pillai (Eds.) *Status and Perspectives in Marine Fisheries Research in India*, Central marine Fisheries Research Institute, Kochi, p. 52 – 114..

Pillai, N.G.K., E.Vivekanandan, U. Ganga and C. Ramachandran. 2009. Marine Fisheries Policy Brief- 1 (Kerala), *CMFRI Spl. Publn*. No. 100, 24p.

Pillay, T.V.R. 1952. A critique of the methods of study of food of fishes. *J. Zool. Soc. India*., 4: 185 – 200.

Pinkas, L., M.S.Oliphant and I. L.K. Iverson. 1971. Food habits of albacore, bluefin tuna and bonito in California waters. *Calif. Fish. Game. Fish, Bull*., 152: 1- 105.

Plaza, G., G. Claramunt and G. Herrera. 2002. An intra-annual analysis of intermediate fecundity, batch fecundity and oocyte size of ripening ovaries of Pacific sardine *Sardinops sagax* in northern Chile. Fish. Sci., 68: 95 – 103.

Poisson, F. and C. Fauvel. 2009. Reproductive dynamics of swordfish (*Xiphias gladius*) in the southwestern Indian Ocean (Reunion Island). Part 1: Oocyte development, sexual maturity and spawning. *Aquat. Living Resour*. 22: 45 – 58.

Pomeroy, L.R. 1980. Detritus and its role as a food resource. *In*: R .S. K. Barnes and K. H. Mann (Eds.) *Fundamentals of aquatic ecosystems*. Blackwell, p. 84 -102.

Poortenar, C.W., S.H.Hooker and N.Sharp. 2001. Assessment of yellowtail kingfish (Seriola lalandi) reproductive physiology, as a basis for aquaculture development. *Aquaculture* 201: 271 – 286.

Prabhu, M. S. 1955. Some aspects of the biology of the ribbonfish *Trichiurus haumela* (Forskkal). *Indian J. Fish*.,2 (1): 132 - 163.

Prabhu, M. S. 1956. Maturation of intra-ovarian eggs and spawning periodicities in some fishes. *Indian J. Fish*.,3: 59 - 90.

Prabhu, M. S. and B.T.Antony Raja, 1959. An instance of hermaphroditism in the Indian mackerel, *Rastrelliger kanagurta* (Cuvier). *Curr.Sci*., 28(2): 73 – 74.

Pradhan, L. B and V. C. Palekar. 1956. Key to the stages of sexual maturity of *Rastrelliger kanagurta* (Cuvier). *Indian J. fish*., 3(1): 183 – 185.

Pradhan, M. J. 1962. Observations on the maturity and spawning of *Psettodes erumei* (Schneider). *Indian J. fish*., 9 (2): 580 – 589.

Prathibha, R and A. C. Gupta. 2004. Fishery, biology and stock of the Indian mackerel *Rastrelliger kanagurta* off Mangalore-Malpe in Karnataka, India. *J. Mar. Biol. Ass. India*., 46(2): 185 – 191.

Priede, I. G. and J. J. Watson. 1993. An evaluation of the daily egg production method for estimating biomass of Atlantic mackerel (*Scomber scombrus*). *Bull. Mar. Sci.*, 53: 891 – 911.

Probst, W. E., Rabeni, C. F., W. G. Covington and R. E. Marteney. 1984. Resource use by stream dwelling rock bass and small-mouth bass. *Trans. Am. Fish. Soc*., 113: 283 – 294.

Prokopchuk, I. and E. Sentyabov. 2006. Diets of herring, mackerel and blue whiting in the Norwegian Sea in relation to *Calanus finmarchus* distribution and temperature conditions. *ICES J.Mar. Sci., J. du Conseil*., 63(1): 117 – 127.

Qasim, S. Z. 1972. The dynamics of the food and feeding habits of some marine fishes. *Indian J. Fish*., 19(1 & 2): 11 - 21.

Qasim, S. Z. 1973. An appraisal of the studies on maturation and spawning in marine teleosts from the Indian waters. *Indian J. Fish*., 20: 166- 181.

Qasim, S. Z. and P. G. Jacob. 1972. The estimation of organic carbon in the stomach contents of some marine fishes. *Indian J. Fish*., 19(1 & 2): 29 -34.

Qasim, S. Z. and V. Sankaranarayanan. 1972. Organic detritus of a tropical estuary. *Mar. Biol*., 15: 193 – 199.

Qasim, S. Z., Sumitra Vijayaraghavan and D.C.V.Easterson. 1973. Caloric values of the ingested food of some marine fishes and prawns. *Indian J.Fish*., 20(2): 318 -325.

Raclot T., R. Groscolas, Y. Cherel. 1998. Fatty acid evidence for the importance of myctophid fishes in the diet of king penguins, *Aptenodytes patagonicus*. *Mar. Biol*., 132: 523 – 533.

Radhakrishnan, N. 1963. Notes on the maturity and spawning of *Opisthopterus tardoore* (Cuvier) at Karwar. *Indian J. Fish*.,10 (1) : 102 - 106.

Radhakrishnan, N. 1965. Observations on the maturity and spawning of Indian mackerel, *Rastrelliger kanagurta* (Cuvier) at Karwar. *Indian J. Fish*., **9**(2)A : 512 - 524.

Rajan, S. 1968. Environmental studies of the Chilka Lake. I. Feeding spectrum of the fishes. *Indian J. Fish*., 11: 521 – 532.

Rajasilta, M. 1992. Relationship between food, fat, sexual maturation and spawning time of Baltic Herring (*Clupea Harengus membras*) in the Archipelago seas. *Can. J. Fish. Aquat. Sci*., **49** : 644-54.

Rangarajan, K. 1971. Maturity and spawning of the snapper *Lutianus kasmira* (Forskal) from the Andaman Sea. *Indian J. Fish*., 18 (1&2): 114 –125.

Ratnayake, W.N. and R.G.Ackman. 1979. Fatty alcohols in Capelin, Herring and Mackerel oils and muscle lipids: 1. Fatty alcohol details linking dietary copepod fat with certain fish depot fats. *Lipids*, 14 (9): 795 – 803.

Raymont, J.E.G. 1983. The major taxa of the marine zooplankton. *In*: Raymont, J.E.G. (Ed.) *Plankton and Productivity in the Oceans*. Vol.2. Pergamon Press, NY, p. 52 – 332.

Recks, M. A. and G.T. Seaborn. 2008. Variation in fatty acid composition among nine forage species from a southeastern US estuarine and nearshore coastal ecosystem. *Fish Physiol. Biochem*., 34: 275 - 287.

Rajaguru,A.R. 1992. Biology of two co-occurring tongue fishes, *Cynoglossus arel* and *C. lida* (Pleuronectiformes: Cynoglossidae), from Indian waters*. Fish. Bull*., 90: 328 – 367.

Raju, G. 1964. Fecundity of the oceanic skipjack *Katsuwonus pelamis* (Linnaeus) of Minicoy. *Proc. Symp. Scombroid Fishes.* Part 2. 725 – 732.

Raju, G. 1964. Studies on the spawning of the oceanic skipjack *Katsuwonus pelamis* (Linnaeus) of Minicoy. *Proc. Symp. Scombroid Fishes*. Part 2. 725 – 732.

Rao, A. C. and L. Krishnan. 2009. Studies on the reproductive biology of the female spiny cheek grouper *Epinephleus diacanthus* (Valenciennes, 1828). *Indian J. Fish*., 56 (2): 87 – 94.

Rao, K.V. Narayana. 1962. Observations on the bionomics of the Indian mackerel, *Rastrelliger kanagurta* (C.) caught in the Lawson's bay, near Waltair, Andhra coast. *Proc. Symp. Scombroid Fishes* , part 2: 574 – 585.

Rao, K.V. Narayana. 1962. An account of ripe ovaries of some Indian tunas. *Proc. Symp. Scombroid Fishes* part 2: 733 – 743.

Rao, K.V. Narayana. 1965. Food of the Indian mackerel *Rastrelliger kanagurta* (Cuvier) taken by drift nets of the Arabian Sea off Vizhinjam, South Kerala. *Indian J. Fish*., 9(2): 530 -541.

Rao, K. V. Narayana and K. P. Rao. 1957. Differences in the food of the young and the adult Indian mackerel, *Rastrelliger kanagurta* (Cuv.). *Nature*, 180: 711 – 712.

Rao, K. Satyanarayana. 1967. Reproductive cycles and lipid levels in *Leiognathus splendens* (Cuvier). *J. mar. biol. Ass. India*, 9: 303 –322.

Rao, K. Virabhadra. 1962. Distribution of the young stages of the mackerel, *Rastrelliger kanagurta* (Cuvier) in the Indian inshore waters. *Proc. Symp. Scombroid Fishes* , part 1: 469 – 482.

Rao, K.V. S. 1983. Maturation and spawning of Lizardfishes (*Saurida* spp.) from northwestern part of Bay of Bengal. *Indian J. Fish*., 30 (1): 27 - 45.

Rao,V. Ramamohana. 1962. A note on a hermaphroditic gonad in the Indian mackerel, *Rastrelliger canagurta* (Cuvier). *J. Mar. Biol.Ass. India*, 4(2): 241 – 243.

Rao, V. Ramamohana. 1967. Spawning behaviour and fecundity of the Indian mackerel *Rastrelliger kanagurta* (Cuvier) at Mangalore *Indian J. Fish*., 14: 171 - 186.

Recks, M. A. and G. T. Seaborn. 2008. Variation in fatty acid composition among nine forage species from a southeastern US estuarine and nearshore coastal ecosystem. *Fish Physiol. Biochem*., 34: 275 – 287.

Ricker, W. E. 1954. Stock and recruitment. *J. Fish. Res. Board Can*., 11: 559 – 623.

Rickman, S. J., N. K. Dulvy, S. Jennings and J. D. Reynolds. 2000. Recruitment variation related to fecundity in marine fishes. *Can. J. Fish. Aquat.Sci*.,57: 116 – 124.

Rideout, R. M., M. P.M. Burton and G. A. Rose. 2000. Observations on mass atresia and skipped spawning in northern Atlantic cod from Smith Sound, New foundland. *J. Fish Biol*., 52: 1429 – 1440.

Rijndsorp, A. D. 1991. Changes in fecundity of female North sea plaice *Pleuronectes platessa* L. *Neth. J. Sea. Res*., 25: 279 – 290.

Rijndsorp, A. D. 1993. Fisheries as a large-scale experiment on life-history evolution: disentangling phenotypic and genetic effects in changes in maturation and reproduction of north sea plaice *Pleuronectes platessa* L. *Oecologia*, 96: 391 – 401.

Roberts, S.B., L. F. Jackson, W. V. King, R. G.Taylor, H. J. Grier and C.V. Sullivan. 1999. Annual reproductive cycle of the common snook: endocrine correlates of maturation. *Trans. Am. Fish. Soc*., 128 (3): 436 – 445.

Robichaud, D.A.,R.W.Wlner and R.F.J. Bailey. 1991. Differential selection of crab *Chironectes opilio* and *Hyas* spp. as prey by sympatric cod *Gadus morhua* and thorny skate *Raja radiata*. *Fish. Bull*., 669 – 680.

Rosa, R., P.R.Costa, and M.L.Nunes. 2004. Effect of sexual maturation on the tissue biochemical composition of *Octopus vulgaris* and *O.delfilippi* (Mollusca: Cephalopoda). *Mar.Biol*., 145: 563 – 574.

Rosa, R., P.R.Costa, N.Bandarra and M.L.Nunes. 2005. Changes in tissue biochemical composition and energy reserves associated with sexual maturation in the ommastrephid suids *Illex coindetii* and *Todaropsis eblanae*. *Biol. Bull*., 208: 100 – 113.

Rothschild, B.J. 1986. Dynamics of marine fish populations. Harvard University Press, Cambridge, London.

Rose, K. A., J. H. Cowan, Jr., K. O. Winemiller, R. A. Myers and R. Hilborn. 2001. Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. *Fish and Fisheries*, 2: 293 – 327.

Sabet, S.S., I.M.Reza, A.F. Bagher and G.Saeed. 2009. Study on sexual maturity and levels of gonad steroid hormones in female kutum *Rutilus frisii kutum* (Kamenskii, 1901) during spawning season from river Sefid-Rood of the southern Caspian sea. *J. Cell and Animal Biology*, 3(11): 208 - 215.

Saito, H., K. Ishihara and T. Murase. 1997. The fatty acid composition in tuna (Bonito, *Euthynnus pelamis*) caught at three different localities from tropics to temperate. *J. Sci. Food Agric*., 73: 53 -59.

Saito, H . and M.Murata. 1998. Origin of the monoene fats in the lipids of some midwater fishes : family myctophidae. *Lipids*: 31: 757 – 763.

Saito, H ., K.Watanabe and T . Murase. 1995. the fatty acid composition characteristic of a highly migratory fish with seasonal variation of docosahexaenoic acid content in lipid of bonito. *Biosci. Biotechnol. Biochem*., 59: 2186 -2188.

Saito, H ., R. Yamashiro, C. Alasalvar and T. Konno 1999. Influence of diet on fatty acids of three sub-tropical fish , subfamily Caesioninae (*Caesio diagramma* and *C.tile*) and family Siganidae (*Siganus canaliculatus*). *Lipids,* 34 (10): 1073 – 1082.

Salonen, K., J.Sarvala, I.Hakala and M.L.V. Ljanen. 1976. The relation of energy and organic carbon in aquatic invertebrates. *Limnol. Oceanogr*., 21: 724 – 730.

Sargent, J.R. 1989. The lipids *In*: J.E.Halver (Ed.) *Fish Nutrition*, Academic Press, 2nd edition, Washington,D.C., pp. 153 – 218.

Sargent, J.R., J.G.Bell , M.V. Bell, R.J. Henderson and D.R.Tocher. 1995. Requirement criteria for essential fatty acids. *J. Appl. Ichthyol*., 11: 183 – 198.

Sargent, J., G. Bell, L. McEvoy, D. Tocher and A. Estevez 1999. Recent developments in the essential fatty acid nutrition of fish. *Aquaculture,* 177: 191 -199.

Sargent, J., R. MacIntosh, A. Bauerismeister and J. H. S.Blaxter. 1979. Assimilation of the wax esters of marine zooplankton by herring (*Clupea harengus*) and rainbow trout (*Salmo gairdnerii*). *Mar. Biol*., 51 : 203 - 207.

Sargent, J.R., D.R.Tocher and J.G.Bell. 2002. The lipids *In*: J.E.Halver and R.W.Hardy (Eds.) *Fish Nutrition*, 3rd edition, Academic Press, Washington,D.C., pp: 182 -259.

Sargent, J. and S. Falk – Petersen. 1981. Ecological investigation on the zooplankton community in Balsfjorden Northern Norway: lipids and fatty acids in *Meganyctiphanes norvegica*, *Thysanoessa raschi* and *T. inermis* during mid winter. *Mar.Biol*., 63: 131 – 137.

Schaefer, K..M. 1987. Reproductive biology of black skipjack, *Euthynnus lineatus*, an eastern Pacific tuna. *Inter-Amer. Trop.Tuna Comm., Bull.,* 19 (2): 165 – 260.

Schaefer, K..M. 1996. Spawning time, frequency and batch fecundity of yellowfin tuna (*Thunnus albacares*) near Clipperton Atoll in the eastern Pacific Ocean. *Fish. Bull*. 94: 98 – 112.

Schaefer, K. M. 1998. Reproductive biology of yellowfin tuna (*Thunnus albacares*) in the eastern Pacific Ocean. *Inter-Amer. Trop. Tuna Comm. Bull*., 21(5): 205 – 221.

Schaefer, L.N., M.E. Platell, F. J. Valesinni and I.C. Potter. 2002. Comparison between the influence of habitat type, season and body sizeon the dietary compositions of fish species in near-shore marine waters. *J. Exp. Mar. Biol. Ecol*., 278: 67 – 92.

Schwalane, K., W.C.Mackay and M.T.Clandinin, 1993. Seasonal dynamics of fatty acid composition in female northern pike (*Esox lucius* L.). *J. Comp. Physiol*., B 163: 277 – 287.

Scott, B.E., G.Marteinsdottir, and P.Wright. 1999. Potential effects of maternal factors on spawning stock-recruitment relationships under varying fishing pressure. *Can. J. Fish. Aquat. Sci.,* 56: 1882 – 1890.

Scott, B.E. G.Marteinsdottir, G.A. Begg, P.Wright, O.S.Kjesbu. 2005. Effects of population size/ age structure, condition and temporal dynamics of spawning on reproductive output in Atlantic cod (*Gadus morhua*). *Ecol. Mod*., 191: 383 – 415.

Sekharan, K.V. 1958. On the south Kanara coastal fishery for mackerel \ (Cuvier) together with notes on the biology of the fish. *Indian J. Fish*., V(1): 1- 31.

Selvaraj, G.s.D. and M.Rajagopalan. 1973. Some observations on the fecundity and spawning habits of the rock cod *Epinephleus tauvina* (Forsskal). *Indian J. Fish*., 20(2): 668 – 671.

Seshappa, G. 1985. On the homogeneity of the mackerel population at Calicut during the years 1969 – 1976 as determined on the basis of C/L, C/W and TL/ SL ratios. *Ind. J. Fish*., 32: 359 – 374.

Sever, T.M., B. Bayhan, M. Bilecenglu and S. Mavili. 2005. Diet composition of juvenile chub mackerel (*Scomber japonicus*) in the Aegean Sea (Izmir Bay, Turkey. *J. Appl. Ichthyology*, 22 (2) 145 – 148.

Shiraishi, T., K. Ohta, A.Yamaguchi, M.Yoda, H.Chuda and M. Matsumaya. 2005. Reproductive parameters of the chub mackerel *Scomber japonicus* estimated from human chorionic gonadotropin-induced final oocyte maturation and ovulation in captivity. *Fish. Sci.*, 71: 531 – 542.

Sholto-Douglas, A.D., J.G.Field, A.G.James and N.J. van der Merwe. 1991. 13C/12C and 15N/14Nisotope ratios in the southern Beneguela ecosystem: indicators of food web relationships among different size of plankton and pelagic fish; differences between fish muscle and bone collagen tisses. Mar. Ecol. Prog. Ser., 78: 23 – 31.

Shulman, G.E. and R.M.Love. 1999. The biochemical ecology of fishes. *In*: A. J. Southward, P. A. Tyler and C. M. Young (eds.) *Advances in Marine Ecology*, Academic Press, 351 p.

Sidell, B.D., E.L.Crockett and W.R.Driedzic. 1995. Antarctic fish tissues preferentially catabolize monoenoic fatty acids. *J. Exp. Zool*., 271: 73 – 81.

Sigurgisladottir,S. and H.Palmadottir. 1993. Fatty acid composition of thirty five Icelandic fish species. *J. Am. Oil chem.. Soc*., 70 (11) 1081 – 1087.

Silva, A., M.B. Santos, B.Caneco, G.Pestana, C.Porteiro, P. Carrera and Y.Stratoudakis. 2006. Temporal and geographic variability of sardine maturity at length in the northeastern Atlantic and western Mediterannean. *ICES J. Mar.Sci*., 63(4): 663 – 674.

Sivadas, M. and M. M. Bhaskaran. 2009. Stomach content analysis of the Indian mackerel Rastrelliger kanagurta (Cuvier) from Calicut, Kerala. *Indian J. fish*., 56(2) 143 – 146.

Sivadas, M., P. N. R. Nair, K. K. Balasubramanian and M. M. Bhaskaran. 2006. Length weight relationship, relative condition, size at first maturity and sex ratio of Indian mackerel *Rastrelliger kanagurta* from Calicut. *J .mar. Biol.Ass. India*, 48(2): 274 – 277.

Smith, B.B. and K. F. Walker. 2004. Spawning dynamics of common carp in the river Murray, south Australia, shown by macroscopic and histological staging of gonads. *J. Fish Biol.,*64: 336 -354

Smith, S. L. and M. Madhupratap. 2005. Mesozooplankton of the Arabian Sea: Patterns influenced by seasons, upwelling and oxygen concentrations. *Prog. Oceanogr*., 65: 214 – 239.

Sorbera, L. A., J. F. Asturiano, M. Carrillo and S. Zanuy. 2001. Effects of polyunsaturated fatty acids and prostaglandins in oocyte maturation in a marine teleost, the European sea bass (*Dicentrarchus labrax*). *Biol. Reprod*., 64: 382 – 389.

Stacey, N. E. 1984. Control of timing of ovulation by exogenous and endogenous factor. *In*: Potts,G.W. and Wooton,R.J.(Eds.) *Fish Reproduction: Strategies and Tactics*, Academic Press, London, pp.207 – 222.

Stacey, N. E. and F. W. Goetz.1982. Role of prostaglandins in fish reproduction. *Can .J. Fish. Aquat. Sci*., 39: 92 -98.

Sterner, R. W. and N. B. George. 2000. Carbon, nitrogen and phosphorous stoichiometry of cyprinid fishes. *Ecology*, 81 (1): 127 – 140.

Strauss, R.E. 1979. Reliability estimates for Ivlev's electivity index, the forage ratio, and a proposed linear index of food selection. *Trans. Am. Fish. Soc*., 108: 344 – 352.

Stratoudakis, Y., M. Bernal, K. Ganias and A. Uriarte. 2006. The daily egg production method: recent advances, current applications and future challenges. *Fish and Fisheries*, 7: 35 – 37.

Sun, B. and N.W. Pankhurst. 2004. Patterns of oocyte growth, vitellogenin and steroid concentrations in greenback flounder. *J. Fish Biol*., 64(5) : 1399 – 1412.

Sundararaj, B.I. 1981. Reproductive physiology of teleost fishes: a review of present knowledge and needs fro further research. Aquaculture development and co-ordination Programme, FAO, U,N., ADCP/REP/16, Rome, pp. 1- 82.

Szedlmayer, S.T. and J.D. Lee. 2004. Diet shifts of juvenile red snapper (*Lutjanus campechanus*) with changes in habitat and fish size. *Fish. Bull*., 102: 366 – 375.

Tessy, K . L. 1994. Studies on the biology of three cultivable species of *Epinephleus* from the south-west coast of India. *Ph.D thesis*, Cochin University of Science and Technology, 219 pp.

Thrush, M. A. and N. R. Bromage. 1991. Relationships between fecundity, egg size, egg volume and fish weight in four stocks of farmed Atlantic Salmon (*Salmo salar*). *In:* Scott,A.P., J.P.Sumpter, D.E. Kinne, M.S, Rolfe (Eds.). *Reproductive physiology of fish*. Fish Symposium 91, Sheffield, U,K,, p. 291.

Tocher, D.R. 2003. Metabolism and functions of lipids and fatty acids in teleost fish. *Reviews in Fisheries Science*, 11(2): 107 -184.

Tocher,D.R. 2010. Fatty acid requirements in ontogeny of marine and freshwater fishh. *Aquaculture Research*, 4(5): 717 – 732.

Tocher, D. R., A. J. Fraser, J. R. Sargent, J.C.Gamble. 1985. Lipid class composition during embryonic and early larval development in Atlantic herring (*Clupea harengus* L.). *Lipids*, 20: 84 -89.

Tocher, D. R. and J.R. Sargent. 1984. Analyses of lipids and fatty acids in ripe roes of some northwest European marine fish. *Lipids*: 492 – 499.

Tomkiewicz, J., L.Tyberg and A.Jespersen. 2003. Micro and macroscopic characteristics to stage gonadal maturation of female Baltic cod. *J. Fish Biol.,* 62: 253- 275.

Townshend, T.J. and R.J. Wootton. 1984. Effects of food supply on the reproduction of the convict cichlid, *Cichalasoma nigrofasciatum*. *J. Fish Biol*., 42: 91 – 104.

Toyomizu, M., T.Nakamura and T.Shono. 1976. Fatty acid composition of lipid from horse mackerel muscle-discussion of fatty acid composition of fish lipid. *Bull. Jap. soc. Sci. fish*., 42(1): 101 -108.

Trippel, E.A. 2003. Estimation of male reproductive success of marine fish. *J. Northw. Atl. Fish. Sci*., 33: 81 – 113.

Trippel, E.A., O.S. Kjesbu and P. Solemdal 1997. Effects of adult age and size structure on reproductive output in marine fishes. *In*: Chambers, R.C., Trippel, E.A. (Eds), *Early Life History and Recruitment in Fish Populations.* Fish and Fisheries Series, vol. 21, Chapman and Hall, London, pp. 31-62.

Turan, H., G. Sonmez and Y. Kaya. 2007. Fatty acid profile and proximate composition of the thornback ray (*Raja clavata*,L.1758) from the sinop coast in the Black Sea. *J. of FisheriesSciences.com* 1 (2): 97 - 103. DOI: 10.3153/jfscom.2007012.

Turner, J.P. and R.Rooker, 2005. Effect of diet on fatty acid composition in *Sciaenops ocellatus*. *J. Fish Biol*., 67: 1119 – 1138.

Tyler, A.V. and R.S.Dunn. 1976. Ration, growth, measures of somatic and organ condition in relation to meal frequency in winter flounder *Pseudopleuronectes americanus* with hypotheses regarding population homeostasis. *J. Fish. Res. Bd. Can*., 33: 63 – 75.

Tyler, C.R. and J.P.Sumpter. 1996. Oocyte growth and development in teleosts. *Rev. Fish Biol. Fish*. 6: 287 – 318.

Udupa, K.S. 1986. Statistical method of estimating the size at first maturity in fishes. *Fishbyte*, 4(2): 8- 10.

Ueda,T. 1976. Changes in the fatty acid composition of mackerel lipid and probably related factors. *Nippon Suisan Gakkaishi*, 42: 479 – 489.

Vallin,L and A.Nissling. 2000. maternal effects o egg size and egg buoyancy of Baltic cod *Gadus morhua*. Implications for stock structure effects on recruitment. *Fish. Res*., 49: 21 -37.

Varljen, J., L. Baticic, G.Sincic- Modric, V.Obersnel, M. Kapovic. 2004. Composition and seasonal variation of fatty acids of *Diplodus vulgaris* L. from the Adriatic Sea. *J. Am. Oil Chem. Soc*., 81 (8): 759 – 763.

Velansky, P.V. and E.Y. Kostetsky. 2008. Lipids of marine cold-water fishes. *Russian Journal of Marine Biology*, 34(1): 51 -56.

Venkataraman, G. 1960. Studies on the food and feeding relationships of the inshore fishes off Calicut on the Malabar coast. *Indian J. Fish*., 7(2): 275 – 306.

Venkataraman, G. and C. Mukundan. 1970. A note on the food of young mackerel. *J. Mar. Biol. Ass. India*., 12(1&2): 230 – 232.

Venkataraman, R. and S.T. Chari. 1951. Seasonal variation in the chemical composition of mackerel *Rastrelliger kanagurta* (Russell). *Proc. Indian Acad. Sci*., 33 (b): 126 –134.

Venkataraman, R., and S.T. Chari. 1953. Studies on mackerel fat variations. Correlation of plankton fat with fat of fish. *Proc. Indian Acad. Sci*., 37 (b): 224 –227.

Vijayaraghavan, P. 1955. Life history and feeding habits of the spotted seer *Scomberomorus guttatus* (Bloch & Schn,). *Indian J. Fish*., 2: 360 – 372.

Vijayaraghavan, P. 1962. Some observation on the spawning behaviour of mackerel. *Indian J. Fish*., 9A (2): 647 –652.

Vivekanandanm, E .2001. Production efficiency of two demersal finfishes in the trawling grounds off Veraval. *Indian J. Fish*., 48(2):123 – 132.

Vivekanandan, E., M.H. Ali and M. Rajagopalan. 2009. Impact of rise in seawater temperature on the spawning of threadfin breams. In: Aggarwal, P.K. (Ed.) Global climate change and Indian Agriculture- Case studies from ICAR Network Project, p. 93 – 96.

Vivekanandan, E., S. Gomathy, P. Thirumilu, M. M. Meiyappan and S. K. Balakumar. 2009. Trophic level of fishes occurring along the Indian coast. *J. Mar. Biol. Ass. India*, 51 (1): 44 – 51.

Vallin, L. and A. Nissling. 2000. maternal effects o egg size and egg buoyancy of Baltic cod *Gadus morhua*. Implications for stock structure effects on recruitment. *Fish. Res*., 49: 21 -37.

Velansky, P.V. and E.Ya. Kostetsky. 2008. Lipids of marine cold-water fishes. *Russian Journal of Marine Biology*, 34(1): 51 – 56.

de Vlaming, V. Oocyte development patterns and hormonal involvements among teleosts.

Vlieg,P. And D.R.Body. 1988. Lipid contents and fatty acid composition of some New Zealand freshwater finfish and marine finfish, shellfish and roes. *New Zealand Journal of Marine and Freshwater Research*, 22: 151 – 162.

Wade, M.G., G. Van Derr Kraak, M.F. Gerrits and J.S.Ballantyne. 1994. Release and steroidogenic actions of polyunsaturated fatty acids in the goldfish testis. *Biol. Reprod*., 51 : 131 – 139.

Wallace, R. and K.Selman. 1981. Cellular and dynamic aspects of the oocyte growth in teleosts. Am. Zool., 21: 325 – 343.

Wallace, R. K. 1981. An assessment of diet-overlap Indexes. *Trans. Am. Fish. Soc.,* 110: 72 - 76.

Walsh, M., P.Hopkins, P.Witthames, P.Greer Walker and N.J. Watson. 1990. Estimation of potential fecundity and atresia in the western mackerel stock, 1989. ICES Document CM 1990/H: 31, 7pp. doi 10.1093/icesjms/fsn216

Walters, C., V. Christensen and D. Pauly. 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Rev. Fish. Biol. Fish*., 7(2): 139 – 172.

Wang, H.Y., H.A.Cook, D.W.Einhouse, D.G.Fielder, K.A.Kayle, L.G. Rudstan and T.O.Hook. 2009. Maturation schedules of walleye populations in the Great Lakes region: comparison of maturation indices and evaluation of sampling-induced biases. *N. Am. J. Fish. Mgmt*., 29: 1540 – 1554.

Ware, D. M. 1975.Relation between egg size, growth, and natural mortality of larval fish.. *J. Fish. Res. Bd. Can.,* 32: 2503 – 2512.

Ware, D.M. 1984.Fitness of different reproductive strategies in teleost fishes. In: G.W.Potts and R.J.Wootton (Eds.) *Fish reproduction strategies and tactics*. Academic Press, New York, p.1 – 12.

Ware, D.M., and R. W.Tanaischuk. 1989. Biological basis of maturation and spawning waves in Pacific herring (*Clupea harengus pallasi*). *Can. J. Fish. Aquat. Sci*., 46: 1776 – 1784.

Watanabe, T.1982. Lipid nutrition in fish. *Comp. Biochem. Physiol*., 73B: 3- 15.

Watanabe, T., T. Murase and H. Saito. 1995. Specificity of fatty acid composition of highly migratory fish. A comparison of docosahexaenoic acid content in total lipids extracted in various organs of bonito (*Euthynnus pelamis*). *Comp. Biochem. Physiol.*, 111 B(4): 691 – 695.

Weber, W. 1974. The influence of hydrographical factors on the spawning time of tropical fish. *In*: K. Tiews (Ed.). *Proc. International Seminar on Fisheries Resources and their management in South east Asia*, Berlin 19 November – 6 December, 1974, p. 269 – 281.

West, G. 1990. Methods of assessing ovarian development in fishes: a review. *Aust. J. Mar. FreshW. Res*., 41: 199 – 222.

Whitehead, C., N. R. Bromage and B. Breton. 1983. Changes in plasma levels of gonadootropins, Oestradiol 17b and vitellogenin during the first and subsequent reproductive cycles of female rainbow trout. *Aquaculture*, 34: 317 – 326.

Wiegand, M. D. 1996. Composition, accumulation and utilization of yolk lipids in teleost fish. *Rev. Fish Biol Fish.*, 6: 259 – 286.

Wiegand, M.D. and D.R. Idler. 1985. Ovarian neutral lipid fatty acid composition varies with state of ovarian growth in landlocked Atlantic salmon. *Can. J. Zool*., 63: 2775 -2777.

Wiegand, M. D. 1982. Vitellogenesis in fishes. *In*: Richter, C.J. and H.J. Goos (Eds.) *Reproductive Physiology of Fish*, p. 136 – 146.

Wiegand, M. D. 1996. Composition, accumulation, and utilization of yolk lipids in teleost fish. *Rev. Fish Biol. Fish.*, 6: 259

Wilkinson, S. G. 1988. Gram negative bacteris. *In*: Ratledge,C., S.G.Wilkinson (Eds.) *Microbial lipids*, Vol.1. Academic Press, London, p. 299 – 488.

Wilson, S. 2002. Nutritional value of detritus and algae in blenny territories on the Great Barrier Reef. *J. Exp. Mar. Biol. Ecol*., 271: 155 – 169.

Wilson, S. K.., K. Burns and S. Codi. 2001. Identifying components of a detritivorous reef fish diet using lipid biomarkers. *Org. Geo. Chem*., 22: 1257 -1269.

Windell, J. T. and S. H. Bowen. 1978. Methods for study of fish diets based on analysis of stomach contents. In: T.Bagenal (Ed.) *Methods for assessment of fish production in fresh waters*, 3rd edition, Oxford: Blackwell Scientific Publication, pp. 227 – 254.

Winemiller, K. O. 1989. Ontogenetic diet shifts and resource partitioning among piscivorous fishes in the Venezualan llanos. *Env. Biol. Fish*., 26: 177 – 199.

Wootton, R. J. 1977. Effect of food limitation during the breeding season on the size, body components and egg production in female sticklebacks *Gasterosteus aculeatus* L. *J. Anim. Ecol*., 46: 823 – 834.

Wootton, R. J. 1979. Energy costs of egg production and environmental determinants of fecundity in teleost fishes. In: P.J. Miller (Ed.) Fish Phenology: Anabolic adaptiveness in teleosts. *Symp. Zool. Soc. Lond*. 44, Academic Press, London, p. 133 – 159.

Wootton, R. J. 1985. Energetics of reproduction. *In*: Tyler, P., Calow, P. (Eds.) *Fish Energetics. New Perspectives*. Croom Helm, London-Sydney, pp. 231 – 254.

Yamada, M. and K. Hayashi. 1975. Fatty acid composition of lipids from 22 species of fish and molluscs. *Bull. Fac. Fish. Hokkaido Univ*., 41 : 1143 – 1152.

Yamada, T., I. Aoki and I. Mitani. 1998. Spawning time, spawning frequency and fecundity of Japanerse chub mackereo *Scomber japonicus* in the waters around Izu islands, Japan. *Fish. Res*., 38 (1): 83 – 89.

Yano,Y., A. Nakayama, H.Saito and K.Ishihara. 1994. Production of docosahexaenoic acid by marine bacteria isolated from deep-sea fish. *Lipids*, 29: 527 – 528.

Yazawa, K. 1996. Production of eicosapentaenoic acid from marine bacteria. *Lipids*, 31: 297 – 300.

Yohannan, T.M. 1979. The growth pattern of Indian mackerel. *Indian J.Fish*., 26 (1&2): 207 – 216.

Yohannan, T.M. 1995. Observations on the spawning of mackerel. *Indian J.Fish*., 40 (3): 197.

Yohannan, T.M. 1997. Biology and fishery of Indian mackerel, *Rastrelliger kanagurta* (Cuvier), along the Malabar coast. *Ph.D. thesis*, Calicut University, 158 pp.

Yohannan, T. M. and U.C. Abdurahiman. 1998. Environmental influence on the behaviour of Indian mackerel and their availability to fishing gear along the Malabar coast. *Indian J.Fish*., 45(3): 239 – 247.

Yohannan,T.M. and U.C.Abdurahiman. 1998a. Maturation and spawning of Indian mackerel. *Indian J.Fish*., 45(4): 399 – 406.

Yohannan,T.M. and P.N.R.Nair. 2002. The resources of Indian mackerel – characteristics, exploitation and future prospects. *In* : N.G.K. Pillai, N.G. Menon, P.P. Pillai and U.Ganga (Eds.) *Management of Scombroid Fisheries*, Central Marine Fisheries Research Institute, Kochi, p. 24 – 32.

Yohannan,T.M. and M. Sivadas. The Indian mackerel. *In*: M.Mohan Joseph and A.A. Jayaprakash (Eds.) *Status of exploited marine fishery resources of India,* Central Marine Fisheries Research Institute, Kochi, p. 60 – 65.

Yohannan, T. M., U. Ganga, Prathiba Rohit, P. P. Pillai, P. N. R.Nair, G. Gopakumar, H. M. Kasim, E. M. Abdussamad, K. Srinivasagan, A. Shanmugavel and M.S. Sumithrudu. 2002. Stock assessment of mackerel in tue Indian seas. *In* : N.G.K .Pillai, N.G. Menon, P.P. Pillai and U Ganga (Eds.) *Management of Scombroid Fisheries*, Central Marine Fisheries Research Institute, Kochi, p. 101 – 106.

Yoshii, K., N. G. Melnik, O. A. Timoshkin, N. A. Bondarenko, P. N. Anoshko, T. Yoshioko and E. Wada. 1999. Stable isotope analyses of the pelagic food web in lake Baikal. *Limnol. Oceanogr.,* 44: 502 – 511.

Young, M., A. Drake, M.Brickhill, J.Farley and T.Carter. 2003. Reproductive dynamics of broad bill sword fish, *Xiphias gladius* in the domestic longline fishery off eastern Australia. *Marine and Freshwater Research*, 54: 315 -332.

Zacharia, P.U. and N.Jayabalan. 2007. Maturation and spawning of the whitefish, *Lactarius lactarius* (Bloch and Schneider, 1801) (family Lactariidae) along the Karnataka coast, India. *J. Mar. Biol. Ass. India*., 49 (2): 166 – 176.

Zanden, vanDer, M. J. and J. B. Rasmunssen. 2001. Variation in N and C trophic fractionation: Implications for aquatic food web studies. *Limnol. Oceanogr*., 46: 2061 -2066.