DURATION AND TIMING OF SPAWNING SEASONS IN MARINE TELEOSTS: A BIOGEOGRAPHICAL APPROACH

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ABSTRACT

The duration and timing patterns of spawning seasons among marine teleosts fishes over broad geographic ranges from the polars to the equator has been reviewed. The review was based on 206 studies in order to evaluate potential patterns of the length or timing of spawning seasons in relation to latitude, habitats and taxonomic groupings patterns. This review confirmed that the timing and duration of spawning of marine teleost fishes is related to latitude. The spawning duration of fishes living in the equatorial region and the tropical regions is generally longer than that of species living in the subtropical and polar regions. With respect to their habitat, in general, the duration and timing patterns of spawning seasons of pelagic fish were not different to demersal fishes.

KEYWORDS: spawn, seasons, duration, marine teleost fish

INTRODUCTION

The duration and timing of spawning seasons vary substantially among marine teleost fishes (Taylor, 1990; Munro *et al.*, 1990). Breeding seasons can range from periods of just a few days (Bye, 1990; Beddow *et al.*, 1998) to all year round (Stequert & Ramcharrun, 1996). Among the seasonal breeders, there is also considerable variation in the time of the year when breeding occurs (Sundararaj, 1981; Longhurst & Pauly, 1987). Some species spawn mainly during summer (Sabates & Martin, 1993), while other spawn during winter (Amara *et al.*, 1994; (Fowler *et al.*, 1999). The processes underlying variation in the duration and timing of spawning seasons are poorly understood. To date there has been no comprehensive review of patterns in the length or timing of spawning seasons, making it difficult to formulate appropriate theories.

The timing and duration of spawning seasons appear to vary with latitude, both within and among species (Taylor, 1990). It is widely assumed that the length of the spawning season increases toward the equator as temperature increases and becomes less variable (Munro *et al.*, 1990). However, there have been no systematic comparisons over a broad latitudinal range to confirm this. Most studies on the spawning seasons of marine fish have been restricted to a single locality and also at high latitude locations. This restricts our ability to determine how single species alter their spawning patterns over potentially broad geographic ranges. However, over recent years, information on the spawning patterns of tropical species has been increasing. There have now been sufficient studies on a range of species from different locations to detect major trends from the polar regions to equatorial environments.

There are several factors that are widely assumed as potential causative factors of the timing of the reproductive season. Photoperiod, temperature, rainfall and food, among other factors, are important in regulating reproductive cycles in teleost fishes (Baggerman, 1990; Taylor, 1990). Many species live over a wide range of latitudes and so encounter different temperature and photoperiod regimes at different locations. This can result in major differences in the timing and duration of reproduction within species (Wootton, 1990). Reproductive seasonality has been well described for high latitude species and is correlated with major seasonal changes in temperature and hours of daylight (Wootton, 1990). Temperature and photoperiod appear to influence both the timing and duration of the spawning season, with most temperate species having restricted spawning periods (Munro *et al.*, 1990). However, strong reproductive seasonality has also been observed at low latitudes in some freshwater and marine species (Bye, 1990; Taylor, 1990). This suggests that the assumption of longer spawning seasons in the tropics may not always apply. Before any conclusions can be drawn, however, a systematic comparison of spawning seasons of different taxa across a wide range of latitudes is necessary.

Marine teleost fishes living in different habitats (e.g. demersal and pelagic fish) experience different abiotic and biotic conditions. Micro climates associated with habitats may also influence reproductive strategies, including

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breeding at a time and place which is most conducive to the survival of their offspring (Bye, 1990). It is thought that pelagic fishes tend to have longer spawning periods than demersal fish. For example the dolphin fish, *Coryhaena hippuru* (Wu *et al*., 2001) and the skipjack tuna, *Katsuwonus pelamis* (Stequert & Ramcharrun, 1996) spawn all year around, while a demersal fish, the Black grouper, *Mcyertoperca bonaci,* spawns over a six month period (Crabtree & Bullock L., 1998). Pelagic fishes are highly mobile and are able to migrate to areas where conditions are optimal for their growth and reproduction. For example, they are able to move to areas where food availability is high, and to warmer areas during winter. In contrast most demersal species are confined to a particular area where local conditions may not always be favourable for reproduction. This was explained why pelagic species are likely to have a longer spawning period than demersal fish. However there are no studies comparing the reproductive timing of fishes living in different habitats over a large geographical scale to help distinguish between the effects of habitat and latitude on the marine teleosts.

The purpose of this review is to draw together information from disparate sources to examine variation in the timing and duration of spawning seasons in marine fishes. The review will evaluate potential patterns in relation to latitude, habitats and taxonomic groupings. The following specific questions will be addressed:

1. Is there a trend toward longer spawning seasons both within and among species from high to low latitude?
2. Is there systematic variation in the timing of spawning both within and among species in relation to latitude?
3. Is there a consistent difference between demersal and pelagic fishes in the duration of spawning seasons?

PATTERNS IN THE DURATION OF SPAWNING PERIOD IN MARINE TELEOSTS WITH RESPECT TO LATITUDINAL RANGE

A through investigation of reproductive studies on marine teleosts from a variety of latitudinal ranges will help us to gain a better understanding on the spawning patterns of marine teleosts across different latitudinal ranges. To examine the relationship between the duration of the spawning season and latitude, I have drawn on 206 studies which mostly conducted between 1993 to 2002 (Table 1).

Table 1. Summary of the duration and timing of spawning seasons in marine teleosts from the polar towards equatorial regions

Species	Month	Spawning season	Latitude	References
Acanthopagrus berda	4	Jun-Sept	17.00 S	(Sheaves *et al*., 1999)
Acanthopagrus schlegeli	4	Jan-Apr	24.00 N	(Huang & Chiu, 1998)
Acanthurus lineatus	5	Oct-Feb	14.00 S	(Craig *et al*., 1997)
Achoerodus Viridis	4	Jul-Oct	33.58 S	(Gillanders, 1995)
Albula vulpes	7	Nov-May	13.11 N	(Crabtree *et al*., 1997b)
Alepochephalus bairdii	4	Jan-Apr	55.00 N	(Allain, 2001)
Amblyglyphidodon leugaster	5	May-Sept	29.30 N	(Goulet, 1995)
Ammodytes hexapterus	2	Sept-Oct	59.17 N	(Robards *et al*., 1999)
Ammodytes marinus	2	Des-Jan	61.00 N	(Bergstad, O. A, 2001)
Anguilla japonica	3	May-Jul	16.00 N	(Ishikawa *et al*., 2001)
Aphanius iberus	7	Mar-Sept	41.00 N	(Vargas & Desostoa, 1996)
Apogon lineatus	4	Jul-Oct	35.00 N	(Kume *et al*., 2000)
Apogon ngripinnis	6	Oct-Mar	26.10 S	(Almeida *et al*., 1999)
Arripis georgiana	2	May-Jun	28 43 S	(Fairclough *et al*., 2000)
Atherina boyeri	8	Feb-Sept	43.10 N	(Tomasini *et al*., 1996)
Atherinomorus lacunosus	5	Aug-Dec	21.00 S	(Conand, 1993)
Athrobucca nibe	8	Sept-Feb/Aug/Mar	30.00 S	(Fennessy, 2000)
Beryx splendens	4	Nov-Feb	20.15 S	(Lehodey *et al*., 1997)
Boreogadus saida	5	Aug-Nov/Feb	80.00 N	(Hop *et al*., 1995)
Brevoortia aurea	5	Sept-Jan	35.00 S	(Acha & Macchi, 2000)
Brevoortia tyrannus	2	Dec-Jan	34.36 N	(Warlen, 1994)

Table 1. Countinous

Species	Month	Spawning season	Latitude	References
Capoeta capoeta umbla	3	Mar-Jul	39.56 N	(Turkmen *et al*., 2001)
Caranx bucculentus	2	Aug-Sept	14.00 N	(Brewer *et al*., 1994)
Caulolatilus princeps	5	Jan-Apr/Aug-Sept	24.45 N	(Garay & Luna, 1994)
Centropomus undecimalis	5	Apr-Aug	27.45 N	(Peters *et al*., 1998)
Centropomus undecimalis	5	May-Sept	27.30 N	(Taylor *et al*., 1998)
Centropristis striata	5	Dec-Apr	28.10 N	(Hood *et al*., 1994)
Centropumus undecimalis	7	Apr-Oct	28.00 N	(Taylor *et al*., 1998)
Centroscyllium fabricii	1	Oct	65.00 S	(Jacobsdottir, 2001)
Cepola rubescens	6	Mar-Oct	39.12 N	(Stergiou *et al*., 1996)
Chelidonichthys kumu	7	Sept-Mar	34.00 S	(Clearwater & Pankhurst, 1994)
Chionodraco hamatus	3	Dec-Feb	60.00 S	(Vacchi *et al*., 1996)
Chionodraco hamatus	3	Jul-Sept	68.30 S	(Vacchi *et al*., 1996)
Choerodon schoenlenii	4	Feb-May	26.17 N	(Ebisawa *et al*., 1995)
Chrypsitera rolandi	12	Jan-Dec	05.00 N	(Srinivasan *et al*., 2002)
Clupea harengus	1	Feb-mar	64.00 N	(Slotte & Fiksen, 2000)
Clupea harengus	2	Feb-mar	64.00 N	(Slotte *et al*., 2000)
Clupea harengus	5	Sept-Jan	54.30 N	(Dickey-Collas *et al*., 2001)
Clupea harengus membras	4	Apr-Jul	60.00 N	(Rajasilta *et al*., 2001)
Clupea harengus membras	5	Apr-Aug	57.00 N	(Anderson *et al*., 2000)
Clupeoid ophistomena	7	Jan-Mar/Jul-Sept	31.00 N	(Acal & Corroespinosa, 1994)
Cnidoglanis macrocephalus	3	Oct-Jan	33.30 S	(Laurenson *et al*., 1993)
Coryhaena hippurus	4	Jul-Sept	36.00 N	(Massuti & Morales-Nin, 1995)
Coryhaena hippurus L	12	Jan-Dec	23.00 N	(Wu *et al*., 2001)
Coryphaenoides rupestris	5	Jun-Nov	56.00 N	(Kelly *et al*., 1996)
Coryphaenoides rupestris	10	Feb-Nov	55.00 N	(Allain, 2001)
Cynoscion regalis	4	May-Aug	37.30 N	(Barbieri *et al*., 1994)
Dascyllus aruanus	4	Jun-Sept	25.00 N	(Mizushima *et al*., 2000)
Decapterus macrosoma	6	Jun-Nov	05.00 N	(Atmaja, S. B. & B. Sadhotomo, 2005)
Decapterus russelli	7	Feb-Aug	05.00 N	(Widodo, J., 1989)
Dentex tumifrons	8	Sept-Des/Mar-Jun	27.30 N	(Oki & Tabeta, 1998)
Dicentrarchus labrax	2	Feb-Mar	40.00 N	(Mananos *et al*., 1997)
Dicologlossa cuneata	5	Jan-May	36.30 N	(Jimenez *et al*., 1998)
Diplodus annularis	5	Jan-May	29.00 N	(Pajuelo & Lorenzo, 2001)
Dosidicus gigas	4	Oct-Jan	05.30 S	(Tafur *et al*., 2001)
Dosidicus gigas	2	Jul-Aug	14.30 S	(Tafur *et al*., 2001)
Engraulis anchoita	4	Mar-Aug	22.30 S	(Lima & Castello, 1995)
Engraulis encrasicolus	6	Mar-Aug	46.00 N	(Motos *et al*., 1996)
Engraulis encrasicolus	2	Jun-Jul	43.30 N	(Nierrmann *et al*., 1994)
Engraulis encrasicolus	3	Jul-Aug	36.30 N	(Millan, 1999)
Engraulis encrasicolus ponticus	4	May-Aug	44.00 N	(Lisovenko & Andrianov, 1996)
Engraulis japonicus	3	Mar-Jun	35.00 N	(Funamoto & Aoki, 2001)
Engraulis japonicus	2	Apr/Jun	34.30 N	(Kim & Nancy, 2001)
Engraulis japonicus	5	Mar-May/Aug-Sept	26.00 N	(Chiu & Chen, 2001)
Engraulis japonicus S	3	Feb-Mar/Jul	26.00 N	(Chiu & Chen, 2001)
Ephinephelus morio	3	Mar-May	22.30 N	(Johnson *et al*., 1998)
Ephinephelus niveatus	6	Apr-Sept	33.30 N	(Wyanski *et al*., 2000)
Ephinephelus polyphekadion	2	Mar-Jun	36.20 S	(Rasem *et al*., 1997)
Epinephelus marginatus	4	Jul-Sept	35.30 N	(Marino *et al*., 2001)
Epinephelus rivulatus	6	Jul-Dec	22.00 S	(Mackie, 2000)

Table 1. Countinous

Species	Month	Spawning season	Latitude	References
Etmopterus princeps	3	Oct/Jun-Jul	65.30 S	(Jacobsdottir, 2001)
Gadus morhua	3	Jan-Mar	52.30 N	(Brander, 1994)
Gadus morhua	3	Apr-Jun	57.30 N	(Anderson *et al*., 1995)
Gadus morhua	3	Apr-Jun	55.00 N	(Kai W. *et al*., 2000)
Gadus morhua	3	Apr-Jun	55.00 N	(Lawson & Rose, 2000)
Gadus morhua	3	Apr-Jun	47.15 N	(Lawson & Rose, 2000)
Gambusia holbrooki	5	May-Sept	41.00 N	(Vargas & Desostoa, 1996)
Gobius roulei	5	Apr-Aug	45.16 N	(Kovacic, 2001)
Halobatrachus didactylus	6	Mar-Aug	36.32 N	(Palazon-Fernandez *et al*., 2001)
Helicolenus dactylopterus	4	Mar-Jun	55.00 N	(Allain, 2001)
Helicolenus dactylopterus	3	Dec-Feb	37.30 N	(Munoz *et al*., 1999)
Hippoglossus hippoglossus	3	Jun,Nov-Dec	44.00 N	(Neilson *et al*., 1993)
Hirundichthys affinis	7	Dec-Jun	13.10 N	(Khokiattiwong *et al*., 2000)
Hucho perryi	1	Jul	51.00 N	(Berg, L. S. *et al*, 1995)
Hucho perryi	1	Apr	47.30 N	(Fukushima, 1994)
Hyperlophus vittatus	5	Mar-Sept	32.55 S	(Gaughan *et al*., 1996)
Hyperoglyphe antartica	3	Mar-May	42.30 S	(Baelde, 1996)
Hypomesus pretiosus japanicus	3	Mar-May	37.30 N	(Hirose & Kawaguchi, 1998)
Johnius amblycephalus	6	Sept-Feb	30.00 S	(Fennessy, 2000)
Johnius dussumieri	6	Sept-Feb	30.00 S	(Fennessy, 2000)
Kaiwarinus equula	6	Mar-Oct	30.00 N	(Yoneda *et* al., 2001a)
Kareius bicoloratus	1	Nov	35.00 N	(Uehara & Shimizu, 1996)
Katsuwonus pelamis	12	Jan-Dec	20.00 S	(Stequert & Ramcharrun, 1996)
Lactophrys quadriconis	6	Jan-Feb/Jul-Sept	10.40 N	(Ruiz *et al*., 1999)
Lates calcarifer	5	Oct-Feb	05.00 N	(Guiguen *et al*., 1994)
Leiognathus brevirostris	2	Feb/Jul	08.00 N	(Jayawardane & Dayaratne, 1998)
Limanda aspera	4	May-Aug	60.05 N	(Paul *et al*., 1993)
Lithognathus lithognathus	2	Mar-Apr	33.00 S	(Bennett, 1993)
Lophiomus setigerus	7	Mar-Nov	30.00 N	(Yoneda *et al*., 1998)
Lophius litulon	4	Feb-May	32.30 N	(Yoneda *et al*., 2001b)
Lutjanus campechanus	2	Mar-Jun	42.13 N	(Soliman M. A. *et al*., 1992)
Lutjanus fulviflamma	6	Dec-Apr	02.00 S	(Kaundaarara & Ntiba, 1997)
Lutjanus vittus	6	Nov-Apr	19.30 N	(Davis & West, 1993)
Megalops atlanticus	4	Apr-Aug	23.35 N	(Crabtree *et al*., 1997a)
Merluccius merluccius	1	Jun	51.30 N	(Fives J. M. *et al*., 2001)
Micromesistius poutassou	1	Apr	51.30 N	(Fives J. M. *et al*., 2001)
Micropogonias undulatus	6	Jun-Des	37.30 N	(Barbieri *et al*., 1994)
Microstomus pacificus	6	Dec-May	45.00 N	(Crone, P. R., 2001)
Mullus barbatus	4	Mar-Jun	33.30 N	(Golani, 1994)
Mycteroperca bonaci	3	Jan-Mar	27.12 N	(Crabtree & Bullock L., 1998)
Mycteroperca bonaci	5	Jan-May	21.30 N	(Garciacagide & Garcia, 1996)
Mycteroperca interstialis	2	Apr-May	28.15 N	(Bullock L. & M. D. Murphy, 1994)
Mycteroperca venenosa	5	Jan-May	21.30 N	(Garciacagide & Garcia, 1996)
Mysteroperca microlepis	3	Feb-Apr	27.00N	(Collins *et al*., 1998)
Odontesthes bonariensis	6	Mar-May/Aug-Oct	25.18S	(Barros & Regidor, 2002)
Opisthonema oglinum	4	May-Aug	21.00 N	(Garcia-Abad *et al*., 1998)
Opisthonema oglinum	6	May-Oct	19.30 N	(Garcia-Abad *et al*., 1998)
Otolithes ruber	6	Sept-Feb	30.00 S	(Fennessy, 2000)

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Species	Month	Spawning season	Latitude	References
Pagellus acarne	5	May-Sept	38.10 N	(Arculeo & Brusle-Sicard, 2000)
Pagellus acarne	6	Oct-Mar	29.00 N	(Pajuelo & Lorenzo, 2000)
Pagrus pagrus	4	Jan-Apr	25.00N	(Hood & Johnson, 2000)
Pampus argenteus	5	Mar-May/Aug-Sept	29.30 N	(Dadzie *et al*., 1998)
Paralabrax maculatofsciatus	3	Jun-Aug	39.00 N	(Allen *et al*., 1995)
Parma microlepis	5	Aug-Jan	34.00 S	(Fowler *et al*., 1999)
Parma microlepis	6	Jul-Nov/Jan	34.30 S	(Tzioumis & Kingsford, 1999)
Peprilus alepidotus	2	Jun-Jul	37.00 N	(Rotunno & Cowen, 1997)
Peprilus burti	6	Feb-May/Sept-Nov	37.00 N	(Rotunno & Cowen, 1997)
Peprilus triacanthus	4	May-Aug	37.00 N	(Rotunno & Cowen, 1997)
Phocoena phocoena	2	Jul-Aug	65.45N	(Lockyer, C. *et al*., 2001)
Platycephalus bassensis	6	Oct-Mar	42.30 S	(Jordan, 2001)
Plectropomus leopardus	3	Sept-Nov	16.39 S	(Ferreira & Russ, 1995)
Pleuronectes platessa	1	Jan	51.00 N	(Arnold & Metcalfe, 1996)
Pleuronectes platessa	3	Feb-Apr	54.00 N	(Ellis & Nash, 1997)
Pomatomus saltatrix	2	Apr-May	45.00 N	(Crone, P. R., 1994)
Pomatomus saltatrix	3	Jul-Sept	41.15 N	(Sabates & Martin, 1993)
Priacanthus macracanthus	2	May-Jun	27.30 N	(Oki & Tabeta, 1999)
Priacanthus macracanthus	4	Apr-Jul	24.45 N	(Liu *et al*., 2001)
Psetta maxima	3	Mar-May	42.30 N	(Caputo *et al*., 2001)
Pseudolabrus celidotus	5	Jul-Nov	38.15 S	(Jones, 1980)
Pseudopercis semifasciata	4	Oct-Jan	47.00 S	(Macchi *et al*., 1995)
Rastrelliger kanagurta	6	Mar-Aug	05.00 N	(Nurhakim, S., 1993)
Reinhardtius hippoglossoides	3	Nov-Jan	73.00 N	(Albert *et al*., 2001)
Repomucenus valenciennei	8	Apr-Nov	35.00 N	(Ikejima & Shimizu, 1999)
Rhincodon typus	2	Apr-May	16.30N	(Heyman *et al*., 2001)
Rhomboplites aurorubens	3	Jun-Aug	32.00 N	(Zhao *et al*., 1997)
Rhomboplites aurorubens	8	Apr-Nov	30.00 N	(Cuellar *et al*., 1996)
Rhomboplites aurorubens	5	Mar-Sept	25.00 N	(Hood & Johnson, 1999)
Salvelinus alpinus	1	Sept	58.00 N	(Beddow *et al*., 1998).
Sardinella aurita	6	Jun-Oct/Dec/Mar	04.00 N	(Quaatey & Maravelias, 1999)
Sardinella maderensis	3	Jan/Apr-May	02.55 N	(Gabche & Hockey, 1995)
Sardinops caeruleus	7	Oct-Apr	28.00 N	(Quinonez-Velaquez *et al*., 2000)
Sardinops melanostictus	1.5	Feb-Mar	32.00 N	(Aoki & Murayama, 1993)
Sarotherodon melanotheron	2	Apr-May	28.00 N	(Faunce, 2000)
sarpa salpa	6	Apr-Sept	30.54 N	(Van Der Walt & B. Q., 1998)
Sciaenops ocellatus	3	Jul-Sept	35.10 N	(Ross *et al*., 1995)
Scomber scombrus	2	Jun-Jul	51.30 N	(Fives J. M. *et al*., 1994)
Scomberomus commerson	2	Oct-Nov	19.00 S	(Mcpherson, 1993)
Scophthalmus rombus	7	Jan-Jul	42.30 N	(Caputo *et al*., 2001)
Sebastolobus macrochir	2	Mar-Apr	45.00 N	(Koya *et al*., 1995)
Selaroides leptolepis	4	Sept-Oct/Jan-Feb	17.30 N	(Venkataramani *et al*., 1995)
Seranus cabrilla	6	Feb-Jul	29.00 N	(Garcia-Diaz *et al*., 1997)
Seriola laladi	1	Des	37.30 S	(Gillanders *et al*., 1999)
Seriolella brama	4	May-Aug	40.00 S	(Knuckey & Sivakumaran, 2001)
Serranus cabrilla	6	Feb-Jul	28.00 N	(Garcia-Diaz *et al*., 1997)
Siganus spinus	3	May-Dec	26.30 N	(Harahap *et al*., 2001)
Siganus sutor	6	Sept-Feb	26.10 S	(Almeida *et al*., 1999)
Sillaginodes punctata	4	Jun-Sept	32.20 S	(Hyndes *et al*., 1998)

Table 1. Countinous

Species	Month	Spawning season	Latitude	References
Sillaginodes punctata	3	Mar-May	34.15 S	(Fowler *et al.*, 1999)
Sillago bassensis	7	Nov-Apr/Sept	32.03 S	(Hyndes & Potter, 1996)
Sillago burrus	3	Dec-Feb	32.15 S	(Hyndes *et al.*, 1996)
Sillago robusta	4	Dec-Mar	32.03 S	(Hyndes & Potter, 1996)
Sillago schomburgkii	3	Dec-Feb	32.15 S	(Hyndes & Potter, 1997)
Sillago vittata	3	Dec-Feb	32.15 S	(Hyndes *et al.*, 1996)
Solea solea	3	Dec-Feb	44.00 N	(Amara, R. *et al.*, 1994)
Sparus auratus	2	Nov-Des	36.40 S	(Zeldis & Francis, 1998)
Sparus auratus	2	Nov-Des	36.40 S	(Zeldis & Francis, 1998)
Spondyliosoma cantharus	2	Jan-Feb	28.00 N	(Pajuelo & Lorenzo, 1999)
Tenualosa toli	6	Mar-Oct	03.30 N	(Blaber *et al.*, 1996)
Theragra chalcograma	6	Feb-Jul	58.00 N	(Hinckley, S., 2001)
Thunnus albacares	2	Jul-Aug	28.55 N	(Lang *et al.*, 1994)
Trematomus bernacchii	2	Oct-Nov	60.00 S	(Vacchi *et al.*, 1996)
Trematomus bernacchii	2	Oct-Nov	68.30 S	(Vacchi *et al.*, 1996)
Trematomus hansoni	3	Dec-Feb	60.00 S	(Vacchi *et al.*, 1996)
Trematomus hansoni	3	Sept-Nov	68.30 S	(Vacchi *et al.*, 1996)
Trichiurus lepturus	4	Mar-Jun	22.00 N	(Kwok & Ni, 1999)
Trichiurus lepturus	4	Nov-Feb	30.00 S	(Martins & Haimovici, 2000)
Trichiurus nanhaiensis	5	Apr-Aug	22.00 N	(Kwok & Ni, 1999)
Trisopterus esmarki	2,5	Mar-May	58.00 N	(Albert, 1994)
Upeneus moluccensis	5	Jul-Oct	20.00 N	(Golani, 1994)
Upeneus pori	7	Apr-Oct	20.00 N	(Golani, 1994)
Urophycis brasiliensis	7	Jul-Des	34.54 S	(Acuna *et al.*, 2000)
Urophycis brasiliensis	7	Jun-Des	31.30 S	(Acuna *et al.*, 2000)
Urophycis brasiliensis	3	Mar-May	31.30 S	(Acuna *et al.*, 2000)
Urophycis brasiliensis	3	Mar-May	34.40 S	(Acuna *et al.*, 2000)

Most teleost fishes have been shown to have seasonal reproduction at all latitudes. Some teleosts living at low latitudes do not show a seasonal reproductive patterns. For example the skipjack, *Katsuwonus pelamis,* (20° N-20° S) (Stequert & Ramcharrun, 1996), the dolphin fish, *Coryhaena hippurus L,*(23° N) (Wu *et al.*, 2001), and the damselfih, *Crypsotera rolandi* (5° S) (Srinivasan *et al.*, 2002) spawn throughout the year. There are also some other species which spawn over a relatively long period, such as the bone fish, *Decpterus macrosoma* (5° N) which spawns for 6 months (June to November) (Atmaja, S. B. & B. Sadhotomo, 2005), and the halfmoon grouper *Ephinephelus rivulatus* (22° S) which spawns for 6 months (July to December) (Mackie, 2000), both of them living in tropical waters.

Not all species living at low latitudes spawn all year around or have longer spawning periods than those living at high latitudes. Some low latitude species can have a fairly short spawning duration e.g the whale shark, *Rhincodon typus,* (16.30° N) and spanish mackerel, *Scomberomus commerson,* (19° S) each spawning for 2 months during spring (Mcpherson, 1993).

To overcome this problem I have grouped studies based on six wider latitudinal ranges. These groupings are: 1) the southern polar zone (60 to 90° S); 2) the northern polar zone (60 to 90° N); 3) the southern temperate zone (30 to 60° S); 4) the northern temperate zone (30 to 60° N); 5) the north tropical zone (15 to 30° N); 6) the south tropical zone (15 to 30° S); and 7) the equatorial zone (15° S to15° N) (Figure 1). There are smaller differences in temperature throughout the year at low latitudes compared to high latitude. Stable environmental properties are likely to provide suitable conditions for both stable growth and reproduction. The equatorial zone (15° S to 15° N) has the smallest daily and annual temperature variation, therefore marine teleosts living in this zone will rarely experience extreme temperature fluctuations.

On average marine teleosts living at lower latitudes (<30°) have longer spawning periods than species living at high latitudes (>30°) (Figure 2).

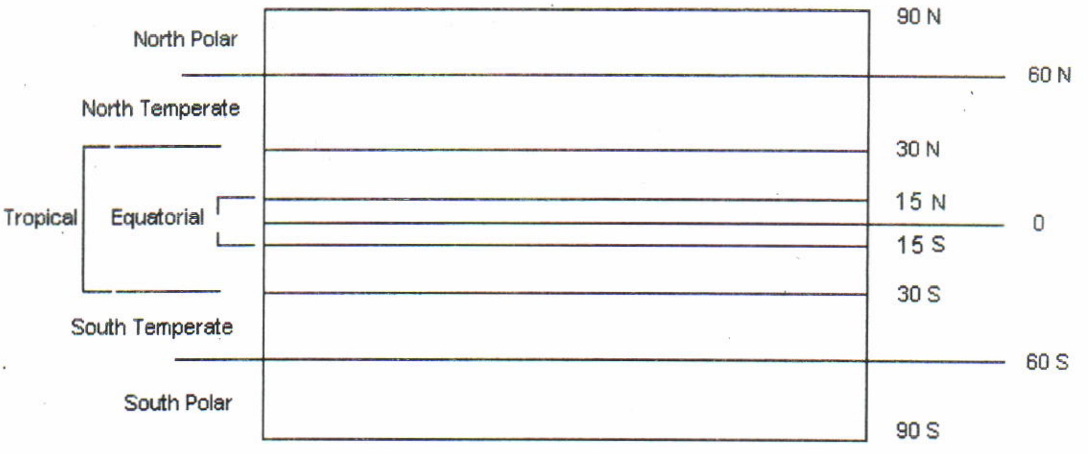

Figure 1. Divisions of Latitudinal range used in this review.

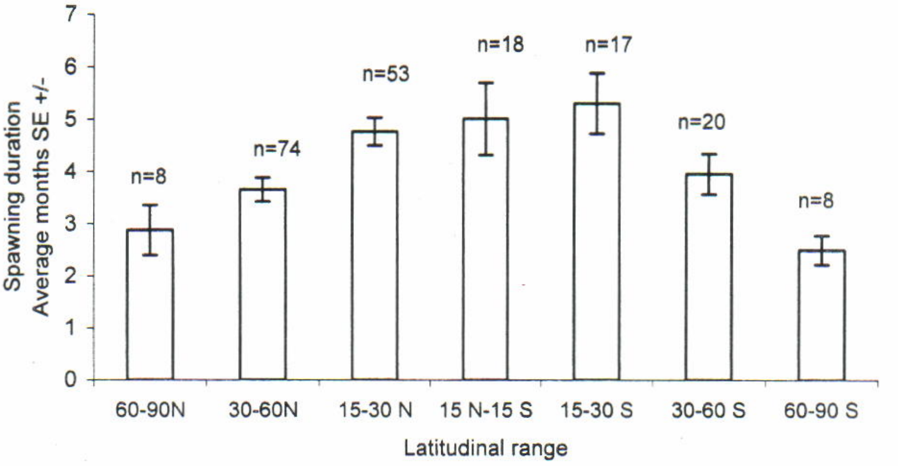

Figure 2. Spawning periods of marine teleosts at different latitudinal ranges (To conform the assumption of using one-way ANOVA test the data were log $_{10}$ transformed).

There was a trend of increasing spawning duration from polar region (60 to 90° N/S) to the equatorial region (15° N to 15° S), and this trend was significant overall (Figure 2, one way ANOVA, F=4,878, p=0.000). Spawning duration of marine teleosts living in the equatorial region, however, was not significantly longer than that of species living in the northern and southern tropical zones (15 to 30° N and 15 to 30° S) (Table 2, Post hoc comparison, p=0.570; p=0.231). This result is probably due to the small number of studies (15) in the 15° N to 15° S zone, with only seven of these close to the equator (i.e. 5° N to 5° S).

Generally, the spawning durations of species living in low latitudes breed longer than species living in sub tropical regions. Up to 43 out of 73 species in the tropical zone have a spawning duration of 5 to 12 months (Table 1). In the equatorial zone (15° N to 15° S) about 13 out of 18 species have a spawning duration of 5 to 12 months with two species were all year round spawners.

Teleost fishes living both in the northern and southern polar regions (60 to 90 N/S) have significantly lower average of spawning durations than those at lower latitudes. Subtropical teleosts fishes (30 to 60 N/S) also show a significant difference in spawning duration compared to the tropical area (15° N to 15° S, 15 to 30° N and 15 to 30° S). Although the exact time of breeding depends on the species, breeding generally starts later at higher latitudes (Baggerman, 1990). This supports the general assumption that in the tropics, marine teleosts are more likely to have a longer spawning period.

The patterns of spawning duration look closely match the pattern in sea surface temperatures (Figure 3). Water temperature reach a peak of 28° C in the tropics and decline below 0°C at the polar

Table 2. Summary of post hoc comparisons of mean spawning duration among the 7 latitudinal ranges (significant value p<0.005). Only significantly different pairs of latitudinal ranges are shown

Latitudinal range	Latitudinal range	p.sig
60-90 N	15-30N	0.008
	15N-15S	0.023
	15-30S	0.005
60-90 S	15-30N	0.002
	15N-15S	0.008
	15-30S	0.002
	30-60S	0.050
30-60 N	15N-15S	0.024

region. In each of the three main oceans (Indian Ocean, Pacific Ocean and Atlantic Ocean, the temperature increases from the poles towards the equator (Figure 3). As the spawning duration of marine teleosts have longer periods in warmer regions i.e. in the tropics than at the polar region (Figure 2.)

Photoperiod and insolation are the two main factors that determine the temperature regimes of the ocean. Photoperiod regimes differ in their duration in different geographical ranges. The tropical area (30° N to 30° S) has a longer light day (8 to 12 h per day) and is relatively stable within a year. Meanwhile in subtropical areas the daylight is shorter in winter than in summer. The polar regions of the Arctic and Antarctic are the coldest receiving less of the sun's radiation than any other part of the earth's surface.

The sea surface temperatures in the tropic are much more stable than pole regions. For example, the annual temperature variation is much greater at the poles (i.e. 20°C) and in the subtropics (i.e. 25°C) than in tropics (i.e. 5°C) (Bigg, 1996). Temperature regimes are also influenced by seasons showing very different patterns between the equatorial and southern northern hemispheres. There are three hypothetical temperatures regimes in these three areas regimes. The equatorial zone exhibits a stable cycle through a year, whereas the southern temperate zone will have a temperature peak at about 35 to 40°C in December (summer) and decreases to the lowest temperature of –5°C in July (winter). Following the opposite pattern, The northern hemisphere exhibits an opposite pattern reaching the lowest temperature of -5°C in December (winter) followed by an increase to the

PATTERNS OF SPAWNING DURATION RELATED TO FOOD AVAILABILITY

Food availability may also affect the spawning duration of teleosts fishes. Differences in the timing of spawning in the Cod (*Gadus morhua*) are not related to temperature but to the timing of plankton production (Brander, 1994). Adequate levels of nutrition must be fulfilled in order to satisfy the animal's physiological condition and ability to complete the reproductive cycle (Nielsen, 1998). The seasonal fluctuations in food availability may determine the timing of reproductive development in some species of teleosts (Collins & Anderson, 1999). Spawning time has been related to fat content which may reflect the importance of food

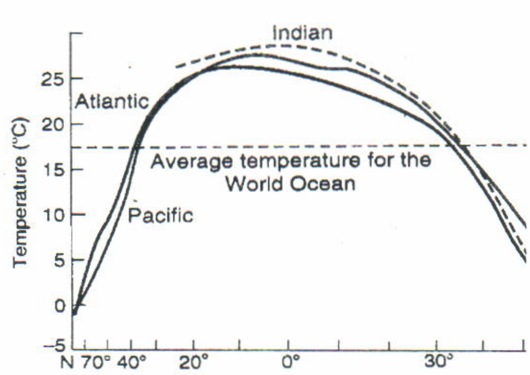

Figure 3. Sea surface temperature in the three major oceans within 70° N to 70° S (Bigg, 1996).

maximum value of 40°C by July (Summer) (Bigg, 1996) (Figure 4).

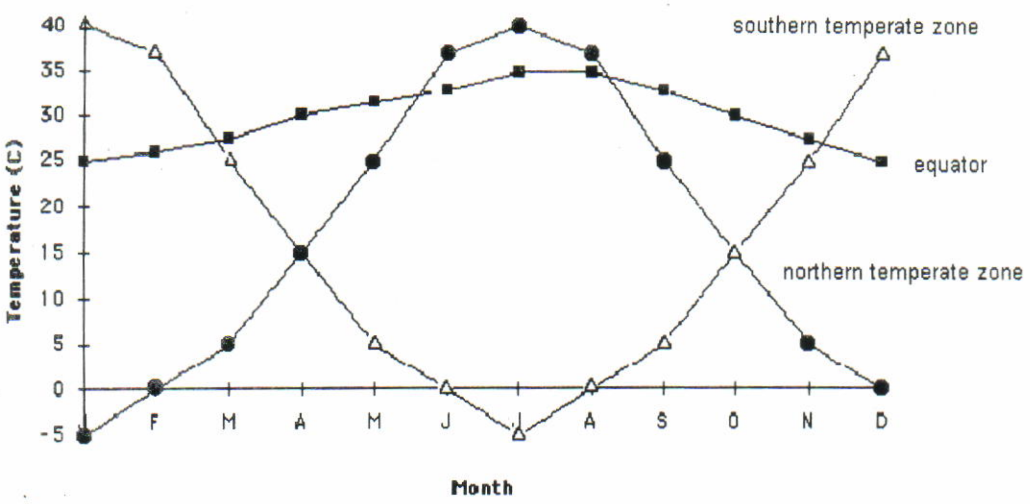

Figure 4. Three hypothetical temperature patterns (equatorial and temperate zones) (Bigg, 1996).

for reproduction. Fish in poor condition (i.e. low fat content) will exhibit delayed maturation (Rajasilta, 1992; Slotte *et al.*, 2000). A restriction on feeding during oocyte recruitment or vitellogenesis, or both, could result in poor condition and thus delay the onset of maturation (Kjesbu *et al.*, 1996), this could also result in fewer maturing females (Bromley *et al.*, 2000) at the start of spawning season.

An increase in food abundance can result in fish storing the maximum energy possible which is accumulated as body fat. This stored energy is to be used for metabolic and reproductive requirements (Paul *et al.*, 1993). A fast increase in body energy/weight indicates that much of the season's energy acquisition takes place in a very short period of intense feeding e.g. 28% of the Yellowfin sole, *Pleuronectes asper,* is accumulated within one month during mid May to mid June, when plankton reaches a peak in abundance (Paul *et al.*, 1993). The spring to autumn energy storage strategy is used by the Yellowfin sole and the Northern flat fish species. Inter annual variations in energy storage can, therefore be related to variation in food abundance (e.g. plankton), and could affect the rate of gamete production (Paul *et al.*, 1993).

Phytoplankton and zooplankton, the main food resources of many marine teleosts, are strongly influenced by season (Munro *et al.*, 1990). Thus the seasonality of plankton abundance will affect both growth and reproduction of planktivorous fish.

In the North Atlantic plankton reaches maximum abundance within March to May and decreases to a minimum during November to February (Figure 5). Some fish species in the Northwest Atlantic spawn mainly during periods of high plankton abundance. For example, in three species of butterfly fish *Peprilus triachantus, Peprilus burti, Peprilus alepidotus* the peak spawning period is March or April (Rotunno & Cowen, 1997). Similarly, some fish in the northeast Atlantic for examples, the Rosefish, *Helicolenus dactylopterus,* and the Roundnose Grenadier, *Coryphaenoides rupestris*, spawn mainly in June which is during the period of peak zooplankton abundance (Allain, 2001).

Plankton abundance in tropical waters is relatively stable throughout the year (Figure 5) (Moyle & Cech, 1996). Therefore planktivorous fish in this region would rarely experience periods of insufficient food. As a result, teleost fishes will be expected to have stable growth and reproduction. The lack of seasonal variation in food availability means that tropical teleosts should have long reproductive periods. In contrast plankton abundance in the polar and subtropical regions is more seasonal. This might affect the growth and reproduction of marine teleosts in this region. During periods of high food abundance, marine teleosts in the subtropical and polar regions grow and store energy as fat. During seasons with low food abundance, fish depend on stored energy for their reproduction.

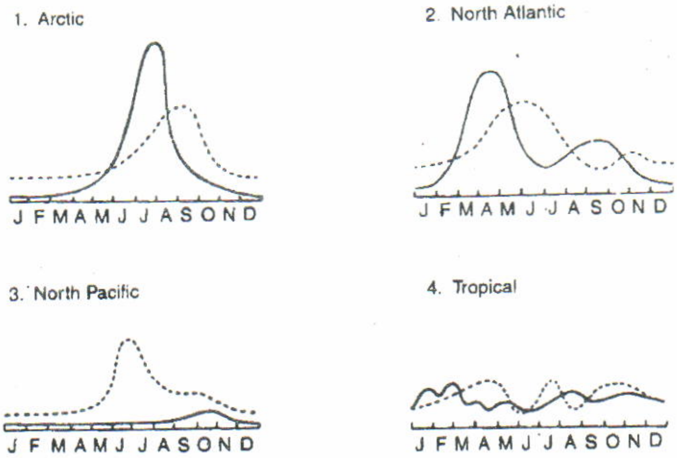

Figure 5. Seasonal productivity in zooplankton and phytoplankton in different parts of the world (Bigg, 1996; Moyle & Cech, 1996) (dot line = zooplankton; solid line = Phytoplankton).

TIMING OF SPAWNING IN RELATION TO LATITUDE

There are considerable differences in the timing of spawning among different latitudes. I attempted to look at this variation by relating the peak spawning time (months) from 206 studies of marine fishes among three broad latitudinal ranges (equatorial (15N to 15S); tropical (15 to 30 N/S) and subtropical (30 to 60 N/S).

A number of trends can be observed from this analysis. The first trend at high latitude, peak spawning periods are generally during spring and summer (i.e. April-July in the northern hemisphere, October to December in the southern hemisphere) (Figure 6). However there are some exceptions, for examples, the Greenland halibut, *Reinhardtius hippoglossoides* at 73^0 N spawns in December-January (Albert *et al.*, 2001); the deepwater squalid shark, *Etmopterus princeps* at 65.30° S spawns in June to July (Jacobsdittir, 2001). The second trend is that teleost fish tend to spawn from January to July (Winte Spring) in the Northern hemisphere within 15 to 30° N. Fishes within 30 to 60° N tend to spawn within June to December (Summer Autumn). Fishes in the south within 15 to 30° S are tend to have more peak spawning within October to December (Spring Summer), while those within 30 to 60° S fishes tend to reach the peak within January to June (Summer Autumn). A the equator (15° N to 15° S) the peak spawning time pattern is difficult to predict because in this region some teleosts fish seem to show the same spawning intensity all year round.

The timing of the onset of spawning is likely to be related to temperature. Some species of marine teleosts are more likely to start earlier their spawning time or increase their breeding activity in warmer temperatures. For example, the red mullet *Mullus barbatus* and the striped mullet, *Mullus surmuletus* in the Mediterranean sea, start spawning 4 weeks earlier than their used to due to the warmer temperatures in their habitat (Golani, 1994). Also the dusky grouper, *Epinephelus marginatus,* at 36° N increases it reproductive output five to eightfold during summer (April to June) and decreases it drastically during winter (December to January) (Marino *et al.*, 2001) as the processes of gonadal development are considerably slowed down by low water temperatures (<8°) (Scott, 1990). Meanwhile the spawning of time of the marine plotosid, *Cnidoglanis macrocephalus* at 28° S, is related to water temperature with a higher temperature of 22° C accelerating the start of spawning by a month compared to the lower temperature of 18° C (Laurenson *et al.*, 1993). Spawning in the bluefish *Pomatomus saltatrix* (L) at around 41° N is limited to the warmest months, from July to September when the surface temperature is about 25° C (Sabates & Martin, 1993). *Lutjanus Vittus* at around 30° N spawns for up to 8 months but reaches its peak within the summer time (Cuellar *et al.*, 1996). These examples provide some evidence to support the idea that marine teleosts are likely to begin spawn in the warmer period.

Photoperiod is also widely known as a factor potentially affecting the spawning time, but its effects vary according to species. For example, constant short photoperiod regimes advanced spawning whereas constant long photoperiod period regimes delayed it in the sea bass, *Dicentrarchus labrax* (Mananos *et al.*, 1997; Prat *et*

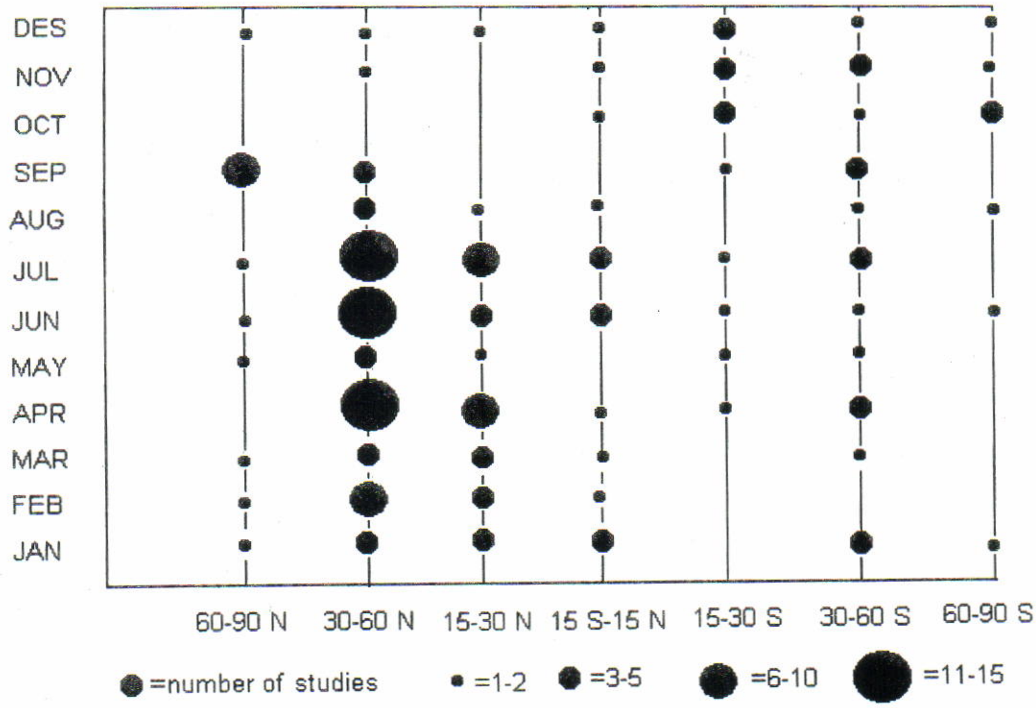

Figure 6. Variability in spawning time within a year in marine teleosts at different latitudes.

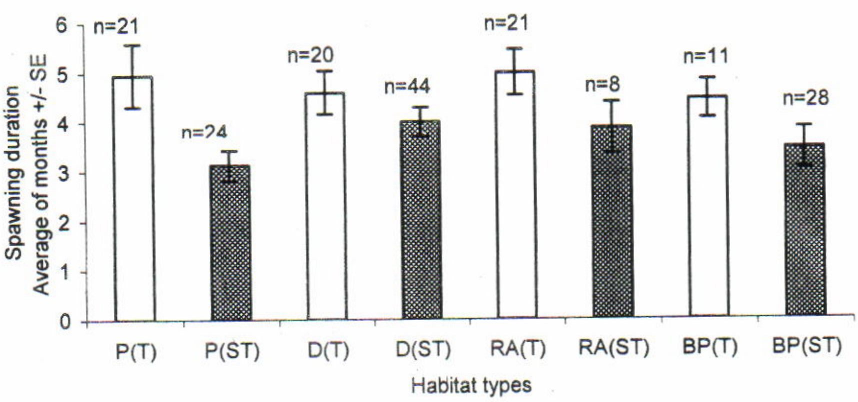

Figure 7. Spawning duration of marine teleosts with respect to habitat between two latitudinal ranges subtropical (30 to 60° S and N), and tropical (30° S–30 ° N).
Remarks: T = Tropical (30° N–30° S); ST = Subtropical (30 to 60° N, 30 to 60° S); P = Pelagic; D = Demersal; RA = Reef associated; BP = bathypelagic; To conform to the assumptions of ANOVA, data were $\log_{10}$ transformed

al., 1999). In contrast, studies on salmonids show the opposite pattern with a delay in the start of spawning by constant short photoperiod and an advance by constant long photoperiod (Takashima & Yamada, 1984). This indicates that photoperiod potentially affects the reproductive timing. However, to validate this assumption more reproductive studies are required to examine the effect of photoperiod on a wider range of species.

DIFFERENCES BETWEEN DEMERSAL AND PELAGIC FISHES IN THEIR PATTERNS OF DURATION OF SPAWNING SEASON

Habitat differences may also be associated with different environmental factors such as temperature, salinity and water pressure as well as food availability. Patterns observed in demersal fish which mostly spend their lifetime close to the sea bed may differ from pelagic fishes which live close to the sea surface. Associated seasonal changes in food availability and water temperature can lead to changes in fish behaviour. Pelagic fish biologically are more likely able to respond to changes by moving from place to place. For example The skipjack tuna, *katsuwonus pelamis*, migrates from the south (20° S) to the north (20° N) in order to inhabit areas with conditions suitable for growth and reproduction (Hunter *et al.*, 1986; Stequert & Ramcharrun, 1996). This result in this species having a relatively long reproductive period. Skipjack tuna spawning occurs throughout the year in tropical waters and seasonally in subtropical waters in all major oceans (Nishikawa *et al.*, 1985). They are oppurtunistic in their reproductive strategy and are thought to spawn throughout their distribution whenever water temperatures rise above 24°C (Schaefer, 2000).

Analysis of spawning durations of pelagic and demersal fishes did not support the prediction that pelagic fish have longer spawning durations (Figure 7, Table 3). This may be due to the fact that not all pelagic fishes are able to increase the length of their spawning season by moving to areas where conditions are favourable. It may also be due to a lack of data for pelagic species.

CONCLUSION

This review confirmed that the timing and duration of spawning of marine teleost fishes is related to latitude. The spawning duration of fishes living in the equatorial region and the tropical regions is generally longer than that of species living in the subtropical and polar regions. In the equatorial peak spawning time is spread throughout the year, whereas at high latitude peak spawning periods were generally during summer. In terms of the spawning duration of marine teleosts with respect to their habitat found that pelagic fish were not different to demersal fishes. The main problem encountered was the paucity of studies on species centred on the equator. More reproductive studies on marine teleosts are still required for equatorial species.

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