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 teleost fishes over broad geographic ranges from the poles 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. Microclimates associated with habitats may also influence reproductive strategies, including...
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, Coryphaena hippurus (Wu et al., 2001) and the skipjack tuna, Katsuwonus pelamis (Stequert & Ramcharrun, 1996) spawn all year around, while a demersal fish, the Black grouper, Mycteroperca 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 SPANNING PERIOD IN MARINE TELEOSTS WITH RESPECT TO LATITUDINAL RANGE**

A thorough 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 schlegelii     | 4         | Jan-Apr         | 24.00 N  | (Huang & Chiu, 1998)  |
| Acanthurus lineatus          | 5         | Oct-Feb         | 14.00 S  | (Craig et al., 1997)  |
| Achoerodus Vindis            | 4         | Jul-Oct         | 33.58 S  | (Gillanders, 1995)    |
| Albula vulpes                | 7         | Nov-May         | 13.11 N  | (Crabtree et al., 1997b) |
| Alepocephalus bairdii        | 4         | Jan-Apr         | 55.00 N  | (Allain, 2001)        |
| Amblyglyphidodon leugaster   | 5         | May-Sept        | 29.30 N  | (Goulet, 1995)        |
| Ammodyclides hexapterus      | 2         | Sept-Oct        | 59.17 N  | (Robards et al., 1999)|
| Ammodyclides 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 nigriminnis           | 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)|
| Atherinonorus lacunosus      | 5         | Aug-Dec         | 21.00 S  | (Conand, 1993)        |
| Athroboucca nive             | 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)        |
# Timing of Sea Season of Spawning

| Species                          | Month      | Spawning season         | Latitude | References                          |
|----------------------------------|------------|-------------------------|----------|-------------------------------------|
| Capoeta capoeta umbra            | 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)                 |
| Centropomus undecimalis          | 7          | Apr-Oct                 | 28.00 N  | (Taylor et al., 1998)               |
| Centrocyllium fabrici           | 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)              |
| Chrysisitera 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)        |
| Clupeoid ophthalmomera           | 7          | Jan-Mar/Jul-Sept        | 31.00 N  | (Acal & Corroespinosa, 1994)        |
| Cnoidoglanis macrocephalus       | 3          | Oct-Jan                 | 33.30 S  | (Laurenson et al., 1993)            |
| Coryphaena hippurus              | 4          | Jul-Sept                | 36.00 N  | (Massuti & Morales-Nin, 1995)       |
| Coryphaena 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)             |
| Dasyccylus 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 tumbrons                  | 8          | Sept-Des/Mar-Jun        | 27.30 N  | (Oki & Tabeta, 1998)                |
| Dicentrarchus labrax             | 2          | Feb-Mar                 | 40.00 N  | (Mananos et al., 1997)              |
| Diploglossa cuneata              | 5          | Jan-May                 | 36.30 N  | (Jimenez et al., 1998)              |
| Diploodus 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  | (Niermann 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 S            | 5          | Mar-May/Aug-Sept        | 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 polypthecadiun      | 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)                      |
| 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 ratei*                | 5          | Apr-Aug               | 46.16 N  | (Kovacic, 2001)                                |
| *Halobatrachus didactylus*    | 6          | Mar-Aug               | 36.32 N  | (Palazon-Fernandez et al., 2001)               |
| *Halicolenus dactylopterus*   | 4          | Mar-Jun               | 55.00 N  | (Allain, 2001)                                 |
| *Hemicolenus 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  | (Khoklatiwong 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  | (Guaghan et al., 1996)                         |
| *Hyperocephale antarctica*    | 3          | Mar-May               | 42.30 S  | (Baelde, 1996)                                 |
| *Hypomesus pretiosus japonicus*| 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 N  | (Fennessy, 2000)                               |
| *Kawarinus equula*            | 11         | Oct-Feb               | 65.00 N  | (Yoneda et al., 2001a)                         |
| *Kareius bicoloratus*         | 11         | Oct-Feb               | 35.00 N  | (Usahara & Shimizu, 1996)                      |
| *Katsuconus pelamis*          | 12         | Jan-Dec               | 20.00 S  | (Stequet & Ramcharrun, 1996)                   |
| *Lactophrys quadricornis*     | 6          | Jan-Feb/Jul-Sept      | 30.40 N  | (Ruiz et al., 1999)                            |
| *Lates calcarifer*            | 5          | Oct-Feb               | 05.00 N  | (Guiguen et al., 1994)                         |
| *Leiognathus brevoirostris*   | 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 N  | (Bennett, 1993)                                |
| *Lophiiformes setigerus*      | 7          | Mar-Nov               | 30.00 N  | (Yoneda et al., 1998)                          |
| *Lophius litoum*              | 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  | (Kaundaara & Nita, 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)                     |
| *Microgogonias undulatus*     | 6          | Jun-Des               | 37.30 N  | (Barbieri et al., 1994)                        |
| *Microstomus pacificus*       | 6          | Dec-May               | 46.00 N  | (Crone, P. R., 2001)                           |
| *Mulius 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  | (Garcia-Cagide & Garcia, 1996)                  |
| *Mycteroperca interstialis*   | 2          | Apr-May               | 28.15 N  | (Bullock L. & M. D. Murphy, 1994)              |
| *Mycteroperca venenosa*       | 5          | Jan-May               | 21.30 N  | (Garcia-Cagide & Garcia, 1996)                  |
| *Mycteroperca microlepis*     | 3          | Feb-Apr               | 27.00 N  | (Collins et al., 1998)                         |
| *Odontesthes bonariensis*     | 6          | Mar-May/Aug-Oct       | 25.18 S  | (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)                               |
| 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                | 25.00 N  | (Hood & Johnson, 2000)                         |
| Pampus argenteus            | 5       | Mar-May/Aug-Sept       | 29.30 N  | (Dadzie et al., 1998)                         |
| Paralabrax maculatofasciatus| 3       | Jun-Aug                | 39.00 N  | (Allen et al., 1995)                          |
| Parma microlepis            | 5       | Aug-Jan                | 34.00    | (Fowler et al., 1999)                         |
| Parma microlepis            | 6       | Jul-Nov/Jan            | 34.30 N  | (Tzioumis & Kingsford, 1999)                   |
| Pepelis alepidotus          | 2       | Jun-Jul                | 37.00 N  | (Rotunno & Cowen, 1997)                       |
| Pepelis burti               | 6       | Feb-May/Sept-Nov       | 37.00 N  | (Rotunno & Cowen, 1997)                       |
| Pepelis triacanthus         | 4       | May-Aug                | 37.00 N  | (Rotunno & Cowen, 1997)                       |
| Phocoena phocoena           | 2       | Jul-Aug                | 65.45 N  | (Lockyer, C. et al., 2001)                     |
| Platychepalus bassensis     | 6       | Oct-Mar                | 42.30    | (Jordan, 2001)                                |
| Plectropomus leopardus      | 3       | Sept-Nov               | 16.39 S  | (Ferreira & Russ, 1995)                        |
| Pleuronectes platessa       | 1       | Jan                    | 51.00    | (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 & Tabela, 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)                         |
| Pseudoabrus celidotus       | 5       | Jul-Nov                | 38.16    | (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)                          |
| Reinhardtus hippocoglossoides| 3      | Nov-Jan                | 73.00 N  | (Albert et al., 2001)                         |
| Repomucenus valenciennae    | 8       | Apr-Nov                | 35.00 N  | (Ikejima & Shimizu, 1999)                     |
| Rhinodontyus               | 2       | Apr-May                | 16.30 N  | (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)                         |
| Sardina aurita             | 6       | Jun-Oct/Dec/Jan        | 04.00 N  | (Quaay & Maravelias, 1999)                    |
| Sardina maderensis         | 3       | Jan/Apr-May            | 02.55 N  | (Gabche & Hockey, 1995)                       |
| Sardinops caeruleus        | 7       | Oct-Apr                | 28.00 N  | (Quinonez-Velazquez et al., 2000)              |
| Sardinops melanosctitus    | 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 rombo           | 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 laiadi             | 1        | Des                   | 37.30    | (Gillanders et al., 1999)                     |
| Seriolaena brama           | 4       | May-Aug                | 40.00 S  | (Knuckey & Sivakumar, 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)         |
| *Spondylosoma canthus*         | 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 hansonii*          | 3       | Dec-Feb         | 60.00 S   | (Vacchi et al., 1996)            |
| *Trematomus hansonii*          | 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   | (Martin & Haimovic, 2000)        |
| *Trichiurus nantaiensis*       | 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) (Stequet & Ramcharrun, 1996), the dolphin fish, *Coryphaena hippurus* L., (23° N) (Wu et al., 2001), and the damselfish, *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, *Decapterus macroso ma* (5° N) which spawns for 6 months (June to November) (Atmaja, S. B. & B. Sadchotomo, 2005), and the hallowed group *Eupinephelus 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, *Scomberomor us commerson*, (19° S) each spawning for 2 months during spring (Mopherson, 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 to 15° 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).
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
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

![Graph](image-url)

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).

![Temperature pattern graph](image)

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

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.
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 (15°N to 15°S); 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 example, the Greenland halibut, Reinhardtius hippoglossoides at 73°N spawns in December-January (Albert et al., 2001); the deepwater squid 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 (Winter 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 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, Cynoglossus 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
The Duration and Timing of A Biogeographical Approach (Fayakun Satria)

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 seabed 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 opportunistic 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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