REPORT

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Is the timing of spawning in sparid fishes a response to sea temperature regimes?

Abstract Published spawning seasons of sparid fish were investigated to determine if there were consistent patterns that could be related to large-scale physical variability, and whether these relationships were species-specific or characteristic of higher taxonomic groupings. For individual species, genera and the family Sparidae as a whole, there was a consistent pattern; spawning at lower latitudes was concentrated close to the month of lowest sea surface temperature, while spawning at higher latitudes was more variable with greater deviations from the month of minimum sea surface temperature. The distribution of sparids may be limited by a lack of tolerance of one or more early life-history stage to high water temperatures, so targeting spawning to the coolest part of the year could be a tactic allowing maximum penetration into warmer waters. Such a link between the physiology of early life-history stages and timing of spawning could have direct consequences for patterns of distributions over a number of taxonomic scales. If there are similar constraints on the reproduction of other species, even minor increases in water temperature due to global warming that may be within the tolerance of adults, may impose constraints on the timing of spawning, with flow-on effects for both species and whole ecosystems.

Keywords Fish · Sparidae · *Acanthopagrus* · *Pagrus* · Spawning

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Introduction

Many events in the reproductive life of fishes occur with clear periodicity, including within-year, within-spawning season, within-lunar cycle, and within-day patterns. The timing of events at each of these scales varies from species to species and from location to location. Some patterns of reproductive timing seem to have obvious explanations. For instance, many species of reef fish aggregate at reef passes to spawn at times of high tidal pressure (Shibuno et al. 1993; Hensley et al. 1994; Domeier and Colin 1997). This is seen as a tactic to direct spawning to a time when eggs and larvae will be washed rapidly away from the reef and its associated high densities of plankton feeding fish (Shibuno et al. 1993; Hensley et al. 1994; Danilowicz 1995). Similarly, in northeastern South Africa (Garratt 1993) the sparid, *Acanthopagrus berda*, spawns in the mouths of estuaries during night time ebb tides. This probably enhances dispersal and may again lead to reduced predation, as eggs are carried away from aggregations of predators in the mouths of the estuaries. The reproduction of *A. berda* also has a clear annual periodicity, with spawning confined to winter months at both locations. In contrast to the timing of tidal periodicity, reasons for this annual pattern are not obvious.

What determines the actual timing of the spawning season of fishes? There are many possible ecological, physiological, and phylogenetic reasons. These are not mutually exclusive, and each category of reasons could operate either through its effect on adults, gametes, eggs, larvae, juveniles, or a combination of these. Ecological factors such as predation, competition, or food availability (quantity or quality), can influence the timing of spawning (Johannes 1978; Norcross and Shaw 1984). For instance, spawning of the herring, *Clupea harengus*, seems to be timed so that larvae hatch at times when phytoplankton abundances are likely to be high (Winters and Wheeler 1996). Alternatively, spawning time may be dictated by physiology. Particular times of the year may

provide the best conditions (e.g., temperature or salinity) for adults to build up body stores that can then be used to elaborate mature gonads. A spawning period during or subsequent to this time would be likely to optimize reproductive output. Perhaps even more likely, spawning may be constrained to coincide with environmental conditions suitable for gametes, eggs or larvae, or targeted so that juveniles are produced at a time when conditions are suitable for survival and growth (Bye 1984; Norcross and Shaw 1984). For instance, spawning of the puffer, *Takifugu niphobles*, is timed to both accommodate the needs of developing embryos and to provide the conditions needed for successful hatching (Yamahira 1997). *T. niphobles* spawns intertidally, and developing embryos need day-time high tides to moderate temperature stress during intertidal incubation. Additionally, to ensure that hatching occurs during periods of submergence, incubation must be completed before neap tides.

The need to target spawning times to accommodate the physiological requirements of early life-history stages can have far reaching implications. For example, it has long been recognised that physiological constraints on spawning can impose limits on the distribution of species (Barnes 1958). The physiological tolerances of a particular life stage may be peculiar to a particular species (Vladic and Järvi 1997) or related to phylogenetic constraints.

Species-specific physiological tolerances have two possible consequences for a species' distribution. If spawning seasons are fixed, for example if they are cued directly to maximum or minimum photoperiod or controlled by a strict circadian rhythm (Follett and Follett 1981), a species' distribution will be limited to areas where the spawning period coincides with suitable environmental conditions. Alternatively, if spawning seasons are not fixed at a particular time of the year, a much broader distribution is possible, with stocks adjusting the timing of spawning to correspond with local optimal environmental conditions. Such an effect has apparently occurred in the gobiid, *Pseudogobius olorum*, which has adjusted its period of spawning to accommodate high summer water temperatures in warm temperate estuaries (Gill et al. 1996).

Rather than being species-specific, the pattern of timing of spawning may be a characteristic of a larger taxonomic group. If so, similar timing should be seen in species throughout the taxonomic group. Clearly, any link between the timing of spawning and environmental variables that is characteristic of higher taxonomic groupings (e.g., families) has considerable implications for the distribution, dispersal and biogeography of that taxon.

This study investigated why fish spawn when they do, with particular emphasis on broad scale relationships between timing of spawning and physical factors for one family of fishes, the Sparidae. Sparids are a speciose and cosmopolitan family of fishes. As well as possessing a circumglobal distribution, sparids can be found over a broad latitudinal range; they occur from temperate to tropical seas (Smith 1965). Because of this broad geographic range, sparids live in, and must spawn under, a variety of combinations of physical conditions. The need to spawn under a diversity of conditions allows the possibility of investigating if and how the timing of spawning (at the species, genus and family level) changes in response to differences in the physical environment.

Three questions were addressed with data obtained from a review of the literature on the spawning seasons of sparid fishes. Firstly, are there consistent spatial differences in the timing of spawning of sparid fishes? Secondly, if there are spatial differences in the timing of spawning can these be related to environmental factors? Thirdly, if the timing of spawning varies spatially and is related to environmental factors, is this a family level pattern or does it carry through to lower taxonomic levels (genus and species)?
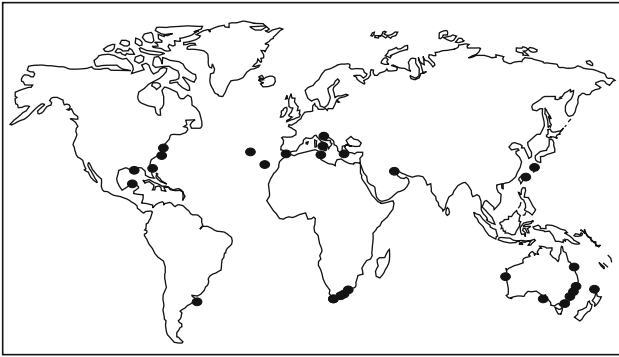
Materials and methods

An extensive literature search was conducted to collect as many records of sparid spawning seasons as possible. Most sources were accounts published in international journals but other reliable sources, such as FAO (Food and Agriculture Organisation) Fisheries Reports and reports of government fisheries organisations, were also used. Only studies that reported year-round gonad maturity data (or at least data including pre-reproductive, reproductive and post-reproductive periods), or studies that made clear statements about peak spawning month(s) or spawning periods were considered. Where original source literature was not available, some secondhand reports were included if they seemed reliable (i.e., were reported secondhand as a quantitative statement) and added to the scope of the data set. Studies with data for part of the spawning period or that reported spawning only to the resolution of a season were not included. The final usable data set comprised 98 records of spawning season, from 82 studies on 23 genera and 49 species and subspecies (Table 1), from a broad cross-section of areas around the world (Fig. 1). Where doubt existed as to the synonymy of species or subspecies they were included separately. Paulin (1990) is followed in using the name *Pagrus auratus*.

Spawning data were reported in many different ways in the studies reviewed. For instance, clear criteria for the start and finish of the spawning period were rarely given, and where they were, the criteria often differed between studies. A single value representing the centre of the spawning season was used to standardise data as much as possible. Where reported, the duration of the spawning season was used to calculate the median spawning month. Where only the peak spawning month was reported, it was assumed to represent the median spawning month. Where both the duration of spawning and peak spawning month were reported, the median spawning month calculated from the duration of spawning

Table 1 Summary of studies providing data on sparid spawning seasons

Genus	Species	Sources
Acanthopagrus	*australis*	Kesteven and Serventy (1941), Pollock (1982)
	berda	Day et al. (1981), Garratt (1993), Kyle (1986 in Garratt 1993), Wallace (1975)
	butcheri	Kailola et al. (1993), Walker and Neira (2001)
	cuvieri	Hussain and Abdullah (1977), Hussain and Saif (1979 in Hussain et al. 1981), Abu-Hakima (1984)
	latus	Hussain and Abdullah (1977), Abu-Hakima (1984)
	schlegeli	Chang and Yeuh (1990), Gwo and Gwo (1993)
Archosargus	*probatocephalus*	Render and Wilson 1992
	rhomboidalis	Charvance et al. (1984)
Argyrozona	*argyrozona*	Brouwer and Griffiths (2005)
Boops	*boops*	Anato and Ktari (1983), Gordo (1995)
Calamus	*leucosteus*	Waltz et al. (1982)
	proridens	Dubovitsky (1977)
Cheimerius	*nufar*	Coetzee (1983), Garratt (1985)
Chrysoblephus	*puniceus*	Garratt (1985)
	cristiceps	Buxton (1990)
	laticeps	Buxton (1990)
Cymatoceps	*nasutus*	Buxton and Clarke (1989)
Dentex	*dentex*	Grubisic (1962 in Glamuzina et al. 1989), Loir et al. (2001)
	gibbosus	Pajuelo and Lorenzo (1995)
Diplodus	*annularis*	Pajuelo and Lorenzo (2001)
	cervinus	Pajuelo et al. (2003)
	sargus	Tortonese (1975 in Micale et al. 1987); Joubert (1981)
	sargus capensis	Coetzee (1986)
	sargus kotschyi	Abou-Seedo et al. (1990)
Lagodon	*rhomboides*	Hildebrand and Schroeder (1928), Hildebrand and Cable (1938 in Darcy 1985), Cody and Bortone (1992)
Lithognathus	*lithognathus*	Mehl (1973), Bennett (1993)
	mormyrus	Lorenzo et al. (2002)
Pachymetopon	*aeneum*	Buxton and Clarke (1986)
	blochii	Pulfrich and Griffiths (1988)
	grande	Buxton and Clarke (1992)
Pagellus	*acarne*	Andaloro (1982 in Neves Santos et al. 1995), Pajuelo and Lorenzo (1994), Neves Santos et al. (1995), Pajuelo and Lorenzo (2000)
	bogaraveo	Krut (1990)
	erythinus	Ghorbel (1981 in Neves Santos et al. 1995); Neves Santos et al. (1995)
Pagrus	*auratus*	Crossland (1977), Scott and Pankhurst (1992), Kailola et al. (1993), Francis (1994)
	caeruleostictus	Chakroun-Marzouk and Kartas (1987)
	major	Sakamoto (1984)
	pagrus	Ranzi (1969 in Manooch and Hassler 1978), Ciechomski and Weiss (1973 in Manooch and Hassler 1978), Manooch (1976 in Manooch and Hassler 1978), Pajuelo and Lorenzo (1996); Hood and Johnson (2000)
Petrus	*rupestris*	Smale (1988)
Polysteganus	*undulosus*	Ahrens (1964 in Garratt 1988), Garratt (1996)
Pterogymnus	*laniarius*	Hecht and Baird (1977), Booth and Buxton (1997)
Rhabdosargus	*holubi*	Wallace (1975)
	sarba	Wallace (1975); Lin et al. (1988 in Leu 1994), El-Agamy (1989), Lin et al. (1990 in Mihelakakis and Kitajima 1995)
Sarpa	*salpa*	Joubert (1981), Anato and Ktari (1983), van der Walt and Mann (1998f)
Sparodon	*durbansensis*	Buxton and Clarke (1991)
Sparus	*aurata*	Arias (1980)
Spondyliosoma	*cantharus*	Pajuelo and Lorenzo (1999)
Stenotomus	*caprinus*	Geoghegan and Chittenden (1982), Sheridan et al. (1984)
	chrysops	Bigelow and Schroeder (1953), Finkelstein (1969a in Geoghegan and Chittenden 1982, Finkelstein (1969b; 1971 in Eklund and Targett 1990)

Fig. 1 Regions (*closed circle*) from which the sparid spawning records used in the study were collected

usually fell in the same month or within 1 month of the peak spawning month. In this case the median calculated from the duration of spawning was used in preference to the peak spawning month because criteria for the designation of peak spawning month were often unclear. Because duration of spawning was often an even number of months, median spawning month often fell between 2 months. Consequently, median spawning month data consisted of 24 half-monthly categories. One species, *Pachymetopon blochii*, was excluded from the analyses. As *P. blochii* is a year round spawner with two spawning peaks (one summer and one winter) (Pulfrich and Griffiths 1988), no clear median spawning month could be calculated.

Spawning data were variously reported at resolutions that ranged from site-specific reports (e.g., a particular estuary) to region-specific reports (e.g., off the coast of a particular country). Except where individual species patterns are considered all data are assumed to relate to a region-specific scale.

Data analysis

For all sites for which there were sparid spawning data, mean monthly sea surface temperature (SST) information was compiled from Halpern et al. (1997, 1998a, b; 1999, 2000, 2001, 2002a, b). These publications referred to the years 1994–2001. For each site the minimum SST and month in which minimum SST occurred was calculated as a mean of the records. The relationship between spawning month and SST was investigated in two ways. Firstly, to consider the full scatter of data, the deviation (in months) of median spawning month from the month of minimum SST was plotted against mean annual SST. This relationship was plotted both for the family (i.e., all data records ignoring genus or species identities), and the genus level for *Acanthopagrus* (20 reports) and *Pagrus* (11 reports), the genera with the most reports of spawning seasons (i.e., all data records for the genus disregarding species identities). Quantile regression, a technique for characterising the boundaries of scatter diagrams that have polygonal shapes (Scharf et al. 1998), was used to estimate the slopes of boundaries of the clouds of

points in the family level scatter plot. The 80th and 20th quantiles were used as the estimates of the upper and lower boundaries, respectively. Because quantile regression involves minimising the sums of absolute residuals, it is resistant to outliers and sparseness in data sets. The approach used was similar to that of Scharf et al. (1998) except that more (1,000) bootstrap samples were used to estimate standard errors and significance levels. At the genus level the data sets were too small for informative quantile regression. Secondly, the mean of the absolute value of deviation (in months) of median spawning month from the month of minimum SST, for each 0.5 increment in mean annual SST, was plotted against mean annual SST. This approach was used to focus on changes in the average variation away from the month of minimum SST. Linear regression was used to investigate the strength of the relationship. The regression was weighted by sample size to account for variations in sample size between increments, thus putting more weight on means that were more precisely estimated and reducing the influence of means based on little data. This approach was applied to both family and genus level data. Because of potential non-independence between family and genus level analyses, the family level analysis was run without the two common genera, *Acanthopagrus* and *Pagrus*. This resulted in no substantial changes in the patterns observed for SST or any other variable.

Similarly, for all latitudes for which there were spawning data, the minimum monthly photoperiod (Linacre 1992) and month of minimum photoperiod were calculated. To investigate the relationship between spawning month and photoperiod, the deviation (in months) of median spawning month from the month of minimum photoperiod was plotted against latitude (per 1°). The family level plot of deviation in spawning month from month of minimum photoperiod against latitude showed a bias towards positive deviations (Fig. 4). To take account of this apparent lagged effect, which could bias the regression result, the relationship was also investigated with deviations calculated relative to the mean of actual deviations (a lag of 1.6 months). Again, the relationships were considered at both the family level and for *Acanthopagrus* and *Pagrus*, with both quantile regression and linear regression approaches used in a parallel way to the analysis of mean SST.

Another physical variable likely to influence spawning month is salinity. However, because salinity varies on spatial scales much smaller than the region-specific resolution of the spawning data, meaningful salinity data at a comparable scale were generally not available. Consequently, regional rainfall data were used as a proxy for seasonal changes in regional salinity. Mean monthly rainfall data (MMR) were compiled from Jackson (1961), Arakawa and Taga (1969), Watts (1969), Arley (1970), Escardo (1970), Griffiths (1972), Schulze (1972), Court (1974), Mosino and Garcia (1974), Prohaska (1976), Cantu (1977) and Taha et al. (1981). For each location the "dry season" was represented by the median month of the longest period below MMR, and the "wet

season" by the median month of the longest period above MMR. Deviations in median spawning month from the median months of the dry and wet seasons were plotted against mean monthly rainfall, mean monthly rainfall during wet months, mean monthly rainfall during dry months and strength of seasonality (mean monthly rainfall of dry/mean monthly rainfall of wet). Again these relationships were considered at both the family level and for *Acanthopagrus* and *Pagrus*, with both quantile regression and linear regression approaches used in a parallel way to the analysis of mean SST.

There were sufficient data to consider the relationships between median spawning month of two species, *Acanthopagrus australis* (four records) and *Pagrus auratus* (six records), and SST and photoperiod at a smaller spatial scale, although the data sets were too small for statistical analysis.

Results

When data for all species are viewed at a family level, deviations in median spawning month from month of minimum SST are distributed fairly evenly before and after the month of minimum SST (Fig. 2). For both the Northern (Fig. 2a) and Southern Hemispheres (Fig. 2b) [and consequently for the combined data set (Fig. 2c)] there is a clear decrease in the deviation of median spawning month away from the month of minimum SST, as mean annual SST increases. At mean annual SSTs of about 20°C and below, the deviation in median spawning month of sparids away from the month of minimum SST varies greatly, with deviations up to 6 months. In contrast, for mean annual SSTs of 21°C and above, the maximum deviation from the month of minimum SST is 3.5 months, with only 3 deviations greater than 2.25 months from a total of 41 data points (Fig. 2c). The reduction in deviation is significant. Quantile regression analysis (Scharf et al. 1998) indicated significant reductions in both the upper (80% quantile: $y = 9.8 - 0.30x$, $P < 0.002$, $n = 88$) and lower (20% quantile: $y = -8.0 + 2.50x$, $P = 0.022$, $n = 88$) boundaries of the data with increasing SST (Fig. 2c). Furthermore, the mean of the absolute value of deviation in spawning month decreased significantly with increasing SST (Table 2; Fig. 3a), reflecting the reduction in deviation with increasing minimum SST. This relationship was strong, as indicated by the high r^2 (0.7677) and large *F*-value (307.43).

The pattern of deviation in median spawning month of sparids from the month of minimum photoperiod (Fig. 4) is similar to that for SST, although not as distinct. At high latitudes there is considerable variation in deviation in median spawning month. At low latitudes the deviation decreases greatly. Again the pattern is similar for both the Northern (Fig. 4a) and Southern Hemispheres. In contrast to the situation for SST, the bulk of
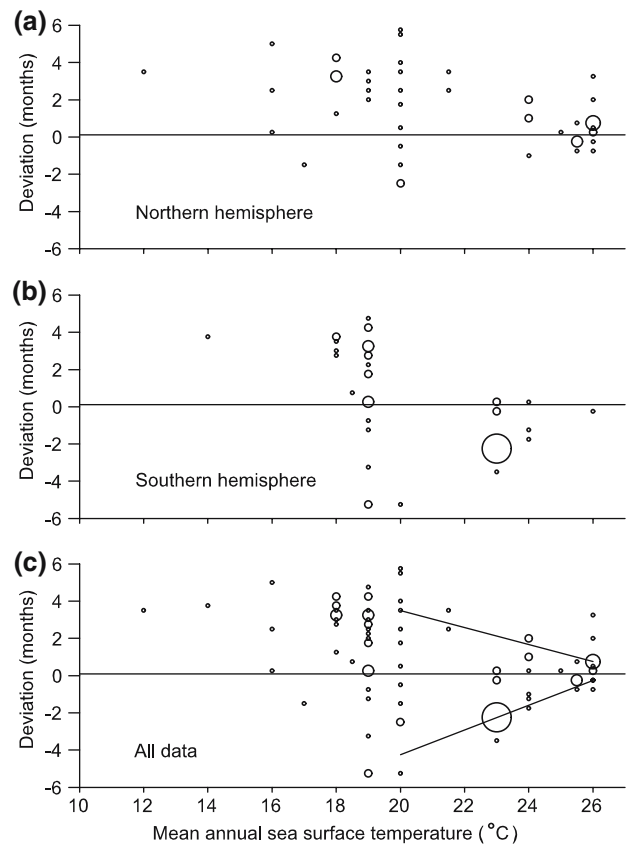

Fig. 2 Deviation in sparid mean spawning month away from the month of minimum sea surface temperature (SST). *Solid lines* on part c represent 80 and 20% quantile regressions describing upper and lower boundaries of the data cloud for SST < 21°C. Bubble sizes are proportion to sample sizes at each point (smallest bubble = 1 point, largest = 8 points). Total $n = 94$

deviations from the month of minimum photoperiod are positive (i.e., after the month of minimum photoperiod). Despite the apparent pattern of decrease towards low latitudes quantile regressions were not significant for either the upper (80%) or lower (20%) quantile boundaries. Again linear regression showed a significant decrease in mean deviation in spawning month from the month of minimum photoperiod towards low latitudes (Table 2; Fig. 3b), although the relationship was not quite as strong as for SST ($r^2 = 0.6244$; $F = 152.92$). The relationship was weaker ($r^2 = 0.4869$; $F = 87.32$) when recalculated to take account of the 1.6 month lag in average deviation after the month of minimum photoperiod (Table 2; Fig. 3c).

Deviation in spawning from mid wet season or mid dry season had significant relationships with most of the rainfall variables investigated (mean monthly rainfall, mean monthly rainfall of wet months, mean monthly rainfall of dry months, or strength of seasonality) (Table 2; Figs. 5, 6), but in all cases the relationships were much weaker than for SST or photoperiod.

Duration of spawning was investigated for the same set of SST, photoperiod and rainfall variables, however,

Fig. 3 Mean deviation in median spawning month (absolute value) away from **a** month of minimum SST, **b** month of minimum photoperiod, **c** month of minimum photoperiod lagged for mean deviation. Bubbles are proportional to sample size
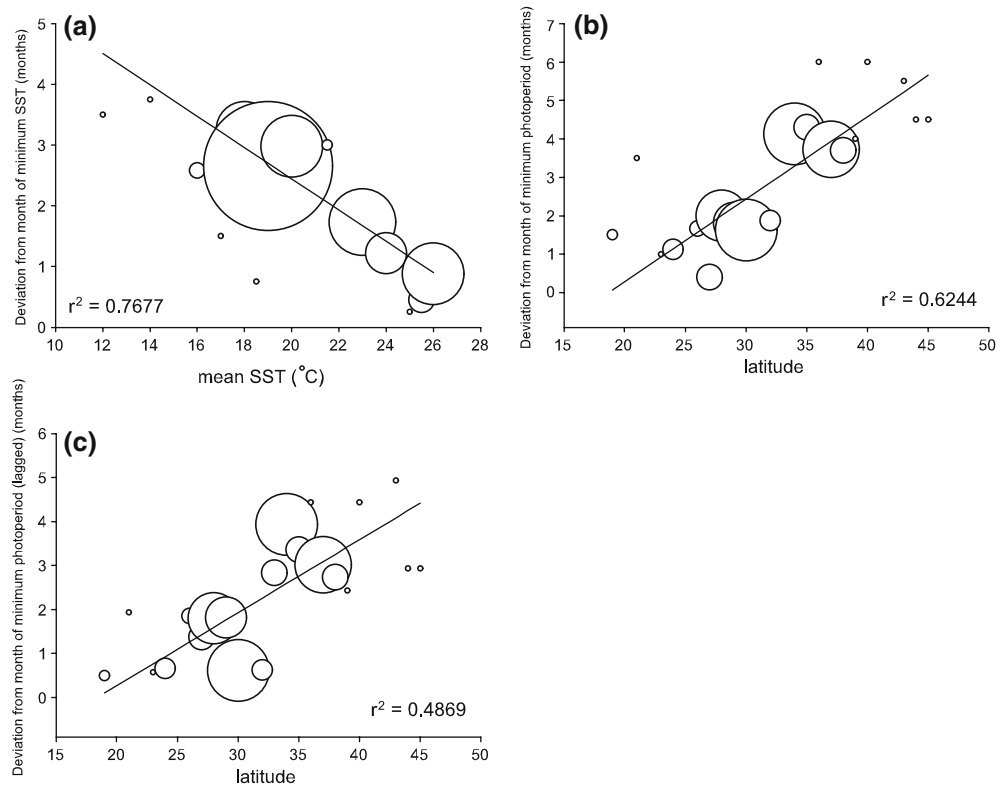

there were no correlations. This is perhaps not surprising given the variable quality of the data available.

The patterns of reducing deviation in spawning month from the month of minimum SST with increasing SST, and decreasing deviation from the month of minimum photoperiod with decreasing latitude, are repeated at the genus level for both *Acanthopagrus* (Table 3; Fig. 7) and *Pagrus* (Table 4; Fig. 8). For *Acanthopagrus* (Fig. 7) the relationship with SST was again the stronger, but for *Pagrus* the relationship with photoperiod was the stronger (Fig. 8).

Data were available for *Acanthopagrus australis* for four sites spanning some 800 km off the east coast of Australia between the Bribie Island/Noosa Heads area and Port Hacking (Fig. 9). There are clear increases in the deviations in median spawning month from both the months of minimum SST and minimum photoperiod, with increasing distance south, towards higher latitudes and lower mean SST. *Pagrus auratus* demonstrate a similar pattern (Fig. 10). In northern spawning populations on both the east and west coast of Australia, there is little deviation in median spawning month from either the month of minimum SST or month of minimum photoperiod. For populations at higher latitudes and lower mean SSTs (southern Australia and New Zealand), there is greater deviation (approx. 3 months) away from the months of minimum SST and minimum photoperiod. Thus the variation in timing of spawning of these two species over their latitudinal and water temperature ranges reflected the patterns at the family and genus levels.

Discussion

There is a clear pattern in the timing of sparid spawning at all taxonomic levels. At the family, genus and species levels, the spawning month of sparids tends to deviate less and less from the months of minimum SST and minimum photoperiod with increases in mean SST and decreases in latitude. At higher latitudes various species of sparids spawn at all times of the year, with peak spawning for some species (e.g., *Cheimerius nufar* for the Port Elizabeth area of South Africa) correlating with maximum sea temperatures and day length (Coetzee 1983). In addition, some individual species (e.g., *Pachymetopon blochii* in the Cape Town area) spawn year round (Pulfrich and Griffiths 1988). At lower latitudes, with higher mean annual SSTs (21°C and above), the situation is quite different, with spawning invariably concentrated in winter months. This pattern is repeated at the genus level. At the species level, in higher latitudes with colder temperatures both *Acanthopagrus australis* and *Pagrus auratus* show greater deviation in spawning month away from the months of minimum temperature and photoperiod than in low latitude locations with higher temperatures. This pattern is replicated on both sides of Australia for *P. auratus*. While there were relationships with rainfall, these were inevitably much weaker than those with temperature and photoperiod. Although rainfall might be an important driver of the timing of spawning it is more parsimonious to suggest that the much weaker relationships simply indicate a
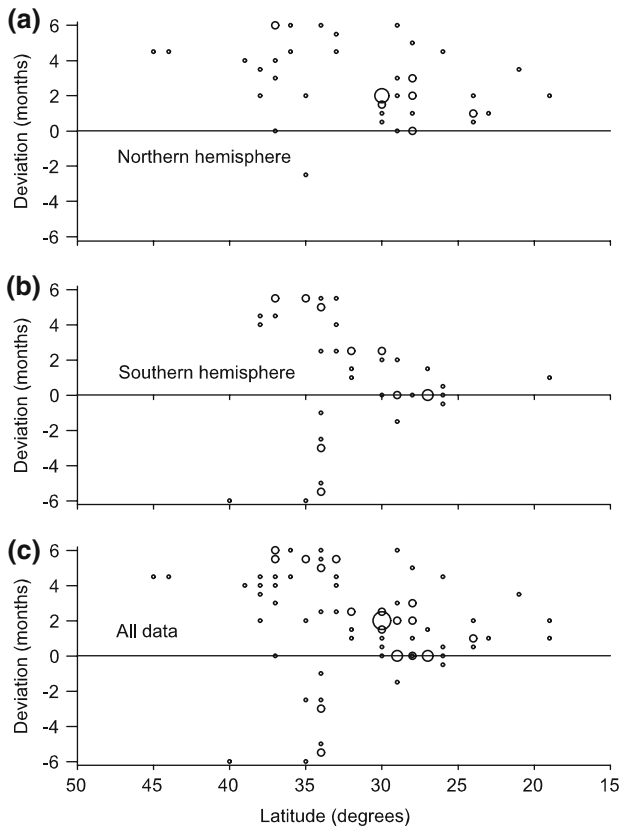
Fig. 4 Deviation in sparid mean spawning month away from the month of minimum photoperiod. Bubble sizes are proportional to sample sizes at each point (smallest bubble = 1 point, largest = 4 points). Total $n = 94$

degree of correlation between rainfall and temperature/latitude.

It is not surprising that timing of spawning seems to be related to temperature and/or photoperiod. Many studies have suggested that one or both of these variables can profoundly influence spawning of fish in general (e.g., de Vlaming 1972; Gill et al. 1996; Mischke and Morris 1997) and sparids in particular (Dubovitsky 1977; Kadmon et al. 1985; Buxton 1990). In fact, for species such as the cyprinid, *Leuciscus leuciscus* (Lobon-Cervia et al. 1996) and the gobiid, *Pseudogobius olorum*,

(Gill et al. 1996), life history tactics may be regulated by the influence of temperature on reproduction. For many temperate teleosts, photoperiod is seen as the most influential environmental determinant of reproductive development (Bromage et al. 2001), with temperature only interacting to synchronize the final stages of maturation (van der Kraak and Pankhurst 1997). However, recent studies suggest this is not necessarily the case, with both the onset and progression of maturation in striped bass, *Morone saxatilis*, regulated by water temperature, even when photoperiod was held constant (Clark et al. 2005). Similarly, water temperature has direct effects on vitellogenesis in other teleosts (Olin and von der Decken 1989; Kim and Takemura 2003), and it has been shown for rainbow trout, *Oncorhynchus mykiss*, that the biochemical mechanisms of Vg mRNA transcription and Vg protein processing do not proceed normally at, inappropriate water temperatures (MacKay and Lazier 1993; MacKay et al. 1996).

The lack of a strong relationship with rainfall (used here as a proxy for salinity) is not remarkable because salinity is usually considered to be less influential in determining the timing of spawning than temperature (Kinne 1964; Bye 1984). For instance, the spawning of *P. olorum* is cued tightly on temperature (*P. olorum* spawns only between 20 and 25°C) but is insensitive to salinity (spawns over a range of salinities from 0.5‰ to more than 30‰) (Gill et al. 1996).

At face value, it appears that the effects of photoperiod and SST on sparid spawning season are completely confounded. This is to be expected because, despite the influence of patterns of oceanic circulation on sea temperature, there is a reasonable correlation between latitude and water temperature. However, there are two reasons for considering SST to be the influential factor. Firstly, except in the case of the genus *Pagrus* where the sample size is small, the relationships between temperature and deviation in spawning month and SST is consistently stronger than that with photoperiod. For mean annual SSTs of 21°C and above (41 records) the maximum deviation from the month of minimum SST is 3.5 months, with most deviations less than 2.25 months. In contrast, even among the eleven records at the lowest

Table 2 Summary of regressions of relationships between absolute deviation in median spawning month away from mean sea surface temperature (SST), photoperiod, and rainfall variables for all sparids

Dependent variable	Independent variable	$F(1/92)$	P	r^2
Deviation from month of min. SST	Mean SST	307.43	3.09×10^{-31}	0.7677
Deviation from month of min. photoperiod	Latitude	152.92	2.86×10^{-21}	0.6244
Mean deviation from month of min. photoperiod (lagged)	Latitude	87.32	5.47×10^{-15}	0.4869
Deviation from mid wet season	Mean monthly rainfall	19.39	0.0001	0.1971
	Mean rainfall wettest months	20.15	0.0001	0.2032
	Mean rainfall driest months	5.96	0.0165	0.0702
	Seasonality	2.95	0.0892	0.0360
Deviation from mid dry season	Mean monthly rainfall	18.68	0.0001	0.1912
	Mean rainfall wettest months	20.53	0.0001	0.2063
	Mean rainfall driest months	4.527	0.0360	0.0542
	Seasonality	1.75	0.1891	0.0216

Fig. 5 Deviation in median spawning month of sparids from median month of wet season versus **a** mean monthly rainfall, **b** mean monthly rainfall of wet months, **c** mean monthly rainfall of dry months, **d** strength of seasonality. Bubbles are proportional to sample size
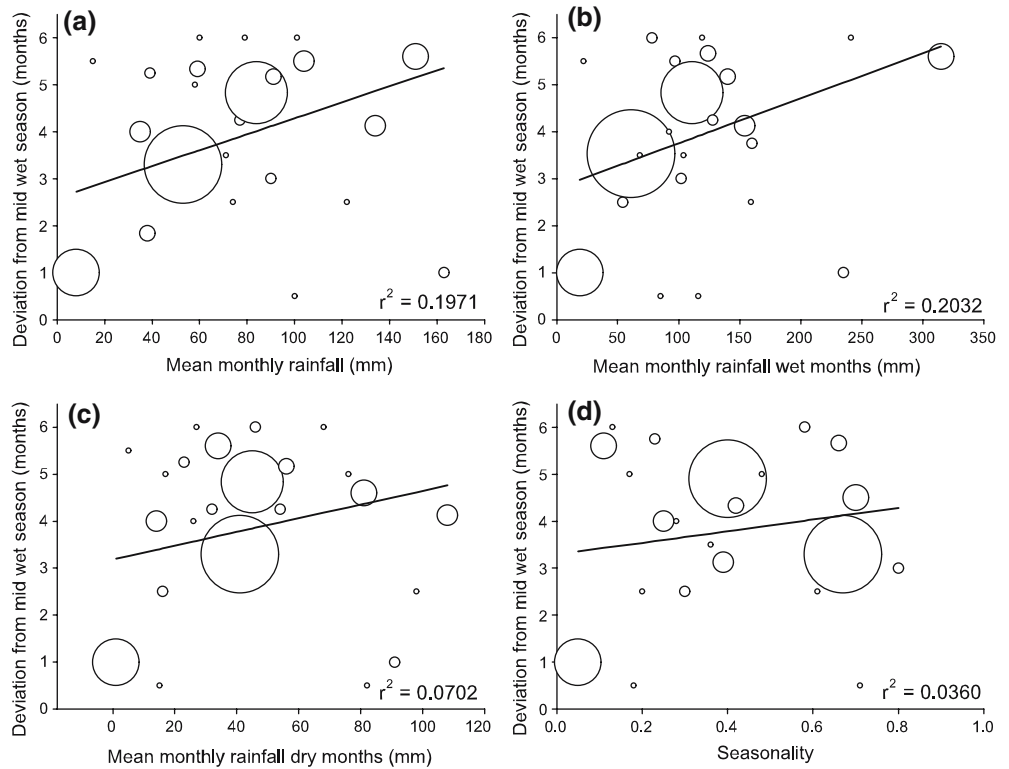
Fig. 6 Deviation in median spawning month of sparids from median month of dry season versus **a** mean monthly rainfall, **b** mean monthly rainfall of wet months, **c** mean monthly rainfall of dry months, **d** strength of seasonality. Bubbles are proportional to sample size

latitudes (26° and below) there were deviations from the month of minimum photoperiod of 4 and 5 months. Considering the possibility of a lag in the spawning/photoperiod relationship weakened, rather than strengthened, the relationship. Secondly, there is evidence for the pre-eminence of temperature in determining the timing of spawning of at least one sparid. In New Zealand waters, the timing of initiation and completion of spawning of *Pagrus auratus* shows interannual variation, but is tightly cued on water temperature; spawning commences
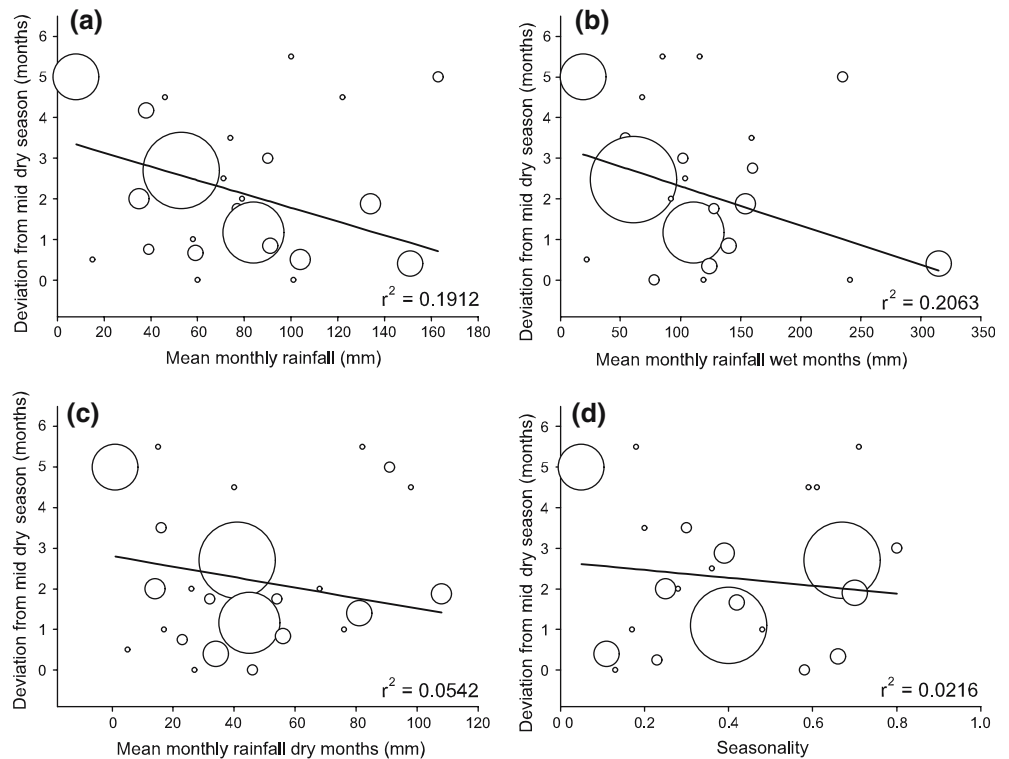
Table 3 Summary of regressions of relationships between absolute deviation in median spawning month away from mean sea surface temperature (SST), photoperiod, and rainfall variables for the genus *Acanthopagrus*

Dependent variable	Independent variable	$F(1/17)$	P	r^2
Deviation from month of min. SST	Mean SST	22.78	0.0002	0.5725
Deviation from month of min. photoperiod	Latitude	11.87	0.0031	0.4111
Deviation from mid wet season	Mean monthly rainfall	1.00	0.3310	0.0556
	Mean rainfall wettest months	3.30	0.0870	0.1626
	Mean rainfall driest months	0.84	0.3717	0.0472
	Seasonality	3.93	0.0640	0.1878
Deviation from mid dry season	Mean monthly rainfall	1.54	0.2320	0.0829
	Mean rainfall wettest months	1.16	0.2959	0.0641
	Mean rainfall driest months	0.99	0.3326	0.0553
	Seasonality	2.98	0.1024	0.1492
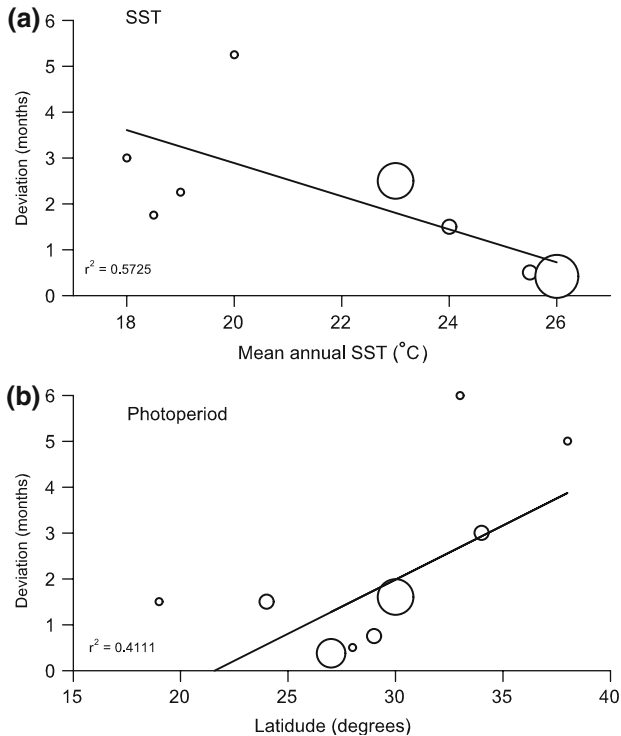
Fig. 7 Deviation in mean spawning month away from **a** the month of minimum sea surface temperature, and **b** the month of minimum photoperiod, for the genus *Acanthopagrus*

at 15°C and finishes at 20°C (Scott and Pankhurst 1992). Tight cueing of spawning to water temperature is not exclusive to *P. auratus;* a number of other sparids also spawn over a small range of temperatures (Manooch 1976; Manooch and Hassler 1978; Charvance et al. 1984).

The relationship between SST and the timing of spawning has been investigated for some species of sparids. Although most authors have linked the timing of spawning to temperature (e.g., Dubovitsky 1977; Buxton 1990), one study found no relationship (Abu-Hakima 1984). Although the study suggesting a lack of relationship was conducted at a tropical location (*Acanthopagrus cuvieri* and *A. latus* in the Arabian Gulf (Abu-Hakima 1984)), it is not at odds with the results presented here because the author assumed that spawning should be

associated with an increase in water temperature and did not consider the possibility of association with a decrease in temperature.

Why should tropical sparids target spawning to the coolest parts of the year when their more temperate counterparts do not? For locations included in the study where mean SSTs were 23°C or above, minimum SSTs ranged from 20–23°C; around the maximum temperature in most sites with mean SST of 20°C or below. Consequently, at the family level, temperatures experienced in winter (at spawning) by more tropical species are close to those experienced during warmer seasons by species in more temperate areas where sparid spawning seasons are more varied. Similarly, at the species level temperatures experienced during winter spawning by warmer water populations of a species are close to those experienced during warm seasons by populations in more temperate areas, where the deviation in spawning from the month of minimum water temperatures is greater. For example, the spawning of *Pagrus auratus* in New Zealand is controlled by temperature, with the initiation of spawn at about 15°C the finish of spawning at about 20°C (Scott and Pankhurst 1992). Here, as in southern Australia, spawning deviates considerably from the month of minimum SST (Fig. 6). Towards the northern limits of the range of *P. auratus* in the Australia/New Zealand region, on the west coast of Australia at Shark Bay, and the east coast of Australia around Moreton Bay, water temperatures only fall to the upper limits of the New Zealand range during the coolest months of the year (Halpern et al. 1997, 1998a, b, 1999, 2000, 2001, 2002a, b). In these areas, the spawning season of *P. auratus* deviates little from the month of minimum SST. Thus, by utilising winter spawning, tropical sparids can spawn over similar temperature ranges to more temperate species and/or populations, albeit at the cost of a shortened reproductive period.

Tropical sparids such as *A. berda* and *A. australis* occur in the same locations (estuaries) throughout the year (Sheaves 1992, 1993, 1998), thus the temperature ranges experienced at these locations remain within adult tolerance levels. Despite this, both species spawn in winter, and in increasingly warmer waters the timing of spawning of *A. australis* moves progressively closer to the month of minimum SST. This, together with the
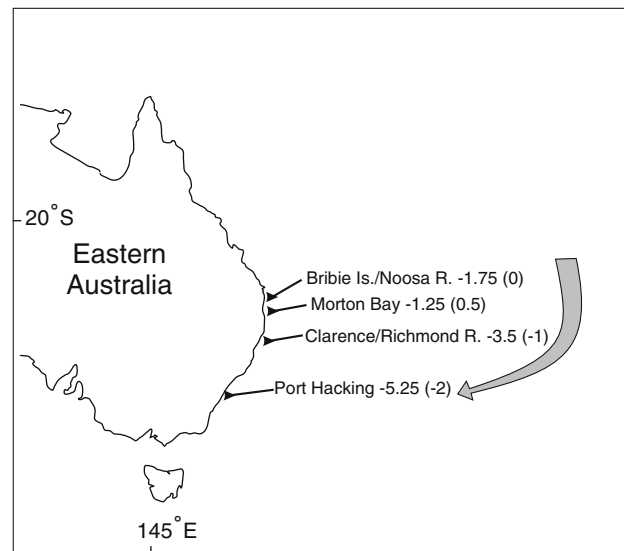
Table 4 Summary of regressions of relationships between absolute deviation in median spawning month away from mean sea surface temperature (SST), photoperiod, and rainfall variables for the genus *Pagrus*

| Dependent variable	Independent variable	F (1/7)	P	r^2
Deviation from month of min. SST	Mean SST	12.06	0.0084	0.6012
Deviation from month of min. photoperiod	Latitude	21.05	0.0018	0.7246
Deviation from mid wet season	Mean monthly rainfall	3.71	0.0953	0.3466
	Mean rainfall wettest months	2.07	0.1937	0.2280
	Mean rainfall driest months	2.39	0.1659	0.2547
	Seasonality	2.14	0.1866	0.2344
Deviation from mid dry season	Mean monthly rainfall	3.35	0.1098	0.3238
	Mean rainfall wettest months	1.29	0.2934	0.1556
	Mean rainfall driest months	2.55	0.1540	0.2674
	Seasonality	2.81	0.1378	0.2862
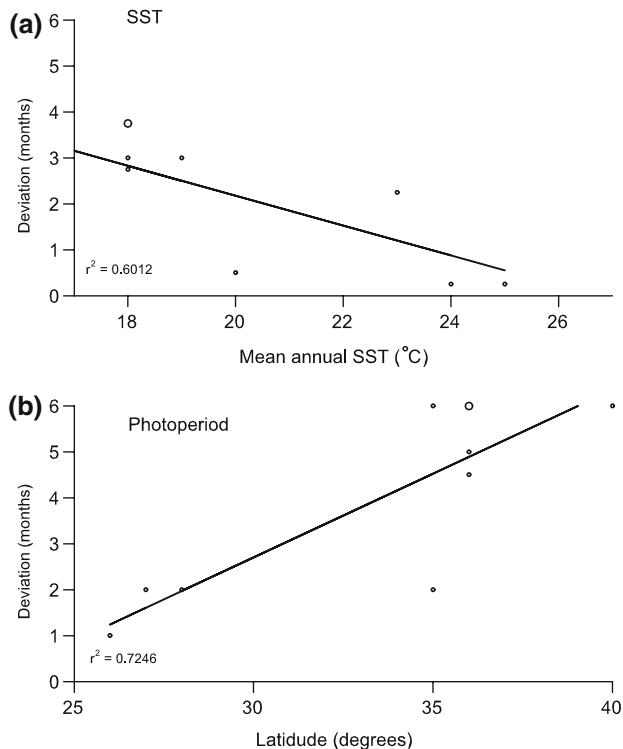
Fig. 8 Deviation in mean spawning month away from **a** the month of minimum sea surface temperature, and **b** the month of minimum photoperiod, the genus *Pagrus*

Fig. 9 Progressive increase in deviation in spawning season from the month of minimum sea surface temperature for *Acanthopagrus australis* with increasing latitude along the east coast of Australia. *Numbers outside brackets* indicate deviation (in months) from the month of minimum sea surface temperature at each site (*negative* denotes spawning peak before the month of minimum sea surface temperature), *numbers in brackets* indicate deviation from the month of minimum photoperiod

family-wide relationship between SST and spawning season, suggests that thermal requirements for gamete development, or gamete, egg or larval survival, rather than thermal requirements of adults, may play an important part in determining the warm water limits of distribution of these species in particular, and sparids in general. If adults possess the physiological ability to withstand high temperatures but gametes, larvae, etc., do not, targeting spawning at times of minimum water temperatures is an obvious tactic to allow a species to maximise penetration into warmer waters. In essence, tropical sparids may be members of a temperate group, limited in distribution by the temperature tolerances of gametes, eggs or larvae, but maximising their penetration into conditions at the upper limits of their thermal tolerance by targeting spawning to times of low water temperature.

Although direct cueing of the timing of reproduction on water temperature to allow the production of gametes, eggs, larvae or juveniles when physical conditions are appropriate is an intriguing and plausible reason for the winter spawning of warmer water sparids, it is not the only possible explanation. Rather than a direct cue to accommodate the physiological needs of early stages, water temperature has often been suggested as a proximate cue that initiates gonad maturation and spawning, so that larvae are produced at times when their planktonic prey are abundant (Bye 1984). For example, the timing of spawning of the osmerid, *Mallotus villosus*, is related to warming sea temperatures that lead to production of larvae when conditions are optimal for zooplankton (Carscadden et al. 1997). Similar suggestions have been made for sparids. For instance, for both *Acanthopagrus butcheri* (Newton 1996) and *Calamus proridens* (Dubovitsky 1977) spawning cues on cold
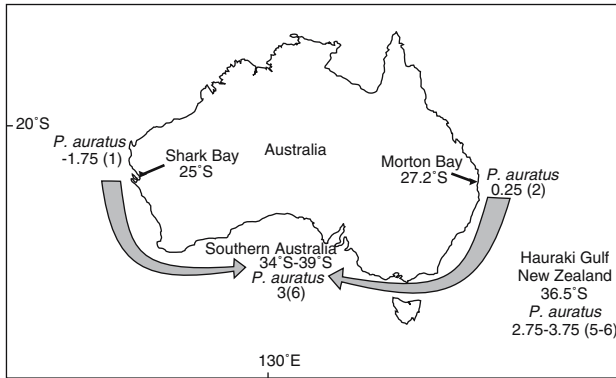
Fig. 10 Progressive increase in deviation in spawning season from the month of minimum sea surface temperature for *Pagrus auratus* with movement south along the coast of Australia. Comparative data for Hauraki Gulf, New Zealand are also provided. *Numbers outside brackets* indicate deviation (in months) from the month of minimum sea surface temperature at each site (*negative* denotes spawning peak before the month of minimum sea surface temperature), *numbers in brackets* indicate deviation from the month of minimum photoperiod. The latitude range to which southern Australia and New Zealand data apply is given

water temperatures leading to larval production at the period of maximum plankton abundance. While it may be the case that the timing of spawning does lead to a match between larval production and plankton productivity, this seems likely to be incidental or of secondary importance in warm water sparids. For this to explain the contraction of the spawning season of warm water sparids to the coolest part of the year, plankton productivity cycles would need to become increasingly seasonal and targeted everywhere to a single time of the year. This does not seem to be the case, because it has long been recognised that in tropical and subtropical areas planktonic productivity is relatively constant and extends over a longer period of the year than in cooler waters (Cushing 1975). On balance, it seems that timing reproduction to allow for the physiological needs of early life-history stages, is a more parsimonious explanation.

Clearly, the links between water temperature, timing of spawning and distribution of sparids suggested here are speculative. Sparids are a speciose and geographically widespread group, and although a strong tendency for sparids to spawn in colder months in areas where water temperatures are higher is evident from the 97 records reviewed here, data were available for only a small proportion of the species-by-location combinations possible. These other combinations provide ample opportunity to test the generality of the pattern described here.

It is tempting to analyse these data in greater detail than has been attempted, but such analyses are probably not warranted. The data available were of variable quality; they were reported in many different ways, and time of spawning was based on data collected using a variety of techniques and judged by a range of criteria. Similarly, the spatial scales that spawning data referred to were variable and sometimes uncertain, so physical variables, such as SST, could only be matched to spawning month

in a general way. Because of such difficulties, further, more detailed studies into the timing of sparid spawning and the forces determining that timing are needed. To do this, careful design, using comparable methods for all species in all areas would be valuable if not crucial. Experimental investigations of the physiological tolerances of young and adult sparids would be of particular value. Even if links between temperature, spawning and the distribution of sparids were established unequivocally, it is unlikely that temperature would act alone. There may be many other important variables which may, and probably do, interact with the effect of water temperature (Bye 1984). Moreover, these interactions, and the relative importance of different variables, would probably vary from place to place and even from time to time.

As with many marine fishes, particularly tropical species (Sheaves 1995; McCormick and Makey 1997), life histories of sparids have not been studied in detail. This is an unfortunate situation because, above all else, the data presented here emphasise that detailed knowledge of life-histories and the requirements of the various life-history stages, may be necessary to account for observed species distributions. Indeed, it may well be that subtle influences at crucial stages may have far reaching impacts on the distribution and abundance of many species. Furthermore, the effect of gamete, egg, larval or juvenile tolerances in constraining the distributions of taxa need not be limited to responses to high temperatures. Equally they could be responses to low temperatures, or the level (or range) of other physical, or indeed biological variables.

Three questions concerning the timing of spawning of fishes were posited in the introduction. To address these: firstly, is seems that for sparids the exact timing of spawning is not an unchanging characteristic of a particular species, but varies over the range of the species. Secondly, it seems that SST is at least correlated with, and probably has an influence on, the timing of spawning in sparids. Thirdly, the relationship between SST and timing of spawning is not just a species level characteristic but is apparent at the levels of genus and family also.

Consequences

Links between the physiology of early life-history stages and timing of spawning could have direct consequences for patterns of distributions over a number of taxonomic scales. However, the consequences of such links could be much more far reaching. For example, global warming is expected to cause substantial increases in water temperature over the next few decades (Parker 1992; Groger and Plag 1993). Even if only the direct effects of temperature rise are considered, and other effects such as changes to hydrological and nutrient cycles (Gucinski et al. 1990) are ignored, the consequences are manifest. To illustrate, the spawning of warm water sparids in winter is quite different to the timing of spawning of many similar tropical fishes, such as lutjanids and serranids (Grimes 1987;

Shapiro 1987; McPherson et al. 1992), which generally show extended spawning over the warmest part of the year (Cushing 1975). What would the effect of global warming be on such species? Species that could not withstand global warming-induced increases in water temperature would be left with two alternatives. Firstly, they could shift their geographic ranges to remain in waters of suitable temperature. Alternatively, if the adults could tolerate the increased water temperatures but gametes, eggs or larvae could not, they could adopt the tactic used by sparids (i.e., spawning in cooler months); as long as they were able to respond fast enough. Indeed, such a response to warming is suggested for the gobiid, *Pseudogobius olorum*. Biannual spawning of *P. olorum* in the Swan Estuary in temperate Western Australia is thought to have developed in response to water temperature rises over the last 10,000 years (Gill et al. 1996). As summer water temperatures increased to a level outside the apparently, rather inflexible spawning temperature range of *P. olorum*, initial summer spawning is thought to have shifted progressively to produce a spring and an autumn spawning period.

If tropical species were forced to shift their spawning season to cooler months, and possibly to reduce the duration of spawning, there could be far reaching consequences for the structure of tropical fish faunas and for tropical fisheries. For example, if timing of spawning and subsequent recruitment changed, reefs or estuaries relying on seasonal hydrographic patterns for larval supply could see impaired recruitment and/or the recruitment of different species (Gucinski et al. 1990). In addition larvae relying on seasonal hydrographic patterns for transport to juvenile habitats, could be transported to inappropriate areas (Norcross and Shaw 1984). This is because the appropriate distribution of eggs and larvae requires precise coupling between spawning and oceanographic transport systems (Norcross and Shaw 1984). Such changes in recruitment patterns could lead to major shifts in fish communities and patterns of biodiversity. The potential implications of global warming induced changes to spawning seasons do not just apply to tropical fishes. For instance, spawning of cooler water species such as haddock, *Merlangius merlangus*, and Norway pout, *Trisopterus esmarkii*, also varies with latitude Hislop (1984), suggesting similar effects are possible.

Changes in the timing of recruitment could have additional consequences for the recruits, and flow-on effects to other taxa. For instance, spawning and subsequent larval production often appears to be timed to match with periods when appropriate food is likely to be abundant (Robertson et al. 1988). Accordingly, changes in the timing of spawning could lead to impaired recruitment due to less certainty in the availability of food for larvae. Downstream consequences for other members of trophic webs are diverse and complex. For example, the time of recruitment of larval fish to many tropical estuaries matches with peak abundances of an important food; mangrove crab larvae (Robertson et al. 1988). Conse-

quently, as well as larval fish arriving at times when food might be in short supply, mortality rates on larval crabs could be greatly reduced. This could in turn lead to enhanced settlement of mangrove crabs and subsequent increased competition between crabs, or allow the opportunity for increases in the abundance of alternative predators of larval crabs.

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