The reproductive biology of intertidal klipfish (Perciformes: Clinidae) in South Africa

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Received 16 May 1994; accepted 30 August 1994

The reproductive biology of six species of viviparous intertidal clinid fish was investigated. Fish were collected monthly from intertidal rock pools between May 1992 and May 1993. Sex ratios varied between 36% female in *Clinus acuminatus* to 53% female in *C. superciliosus*, although this was only significantly different from a 50:50 ratio in *C. acuminatus* (χ^2; $p<0,05$). Size at maturity was greater in females than males of all species and was related to maximium attainable size. Gonad mass varied between 2,6% and 11,6% body mass in males, in males, and reached a maximum of 27,9% in females of *C. agilis*. In five of the species studied, increases in relative gonad mass of males from March to August were followed by increases in gonad mass of females between September and February, suggesting a gestation period of 4–6 months. Only *C. superciliosus* indicated no seasonal trends in gonad development. Juveniles recruited to intertidal rock pools in summer at a total length of between 20 and 25 mm. Up to nine broods of eggs and embryos of different ages were found in the gonads at one time, although there was no relationship between the number of broods and fish size. The total number of reproductive elements (eggs and embryos), however, increased with fish mass in all species. Reproductive potential, calculated as the mean number of broods per mature female multiplied by the mean number of reproductive elements per female, varied from a high of 2843 in *C. acuminatus* to 237 in *Muraenoclinus dorsalis.*

Die voortplantingsbiologie van ses vivipare clinide tussengetyvisspesies is ondersoek. Visse is maandeliks versamel van tussengetyrotspoele van Mei 1992 tot Mei 1993. Geslagsverhoudings het gewissel tussen 36% vroulik in *Clinus acuminatus* tot 53% vroulik in *C. superciliosus*, alhoewel dit slegs in die geval van *C. acuminatus* betekenisvol verskil het van 'n 50:50 verhouding (χ^2; $p<0,05$). Volwasse wyfies was groter as mannetjies in al die spesies, en hul groottes was verwant aan die maksimum bereikbare grootte. Gonademassa het gewissel tussen 2,6 en 11,6% van liggaamsmassa in mannetjies, en het 'n maksimum van 27,9% bereik in wyfies van *C. agilis*. In vyf van die bestudeerde spesies is toenames in die relatiewe gonademassa van mannetjies van Maart tot April gevolg deur toenames in gonademassa van wyfies tussen September en Februarie, wat op 'n dratyd van 4–6 maande dui. Slegs *C. superciliosus* het geen seisoenale neigings in gonadeontwikkeling getoon nie. Onvolwasse visse het die tussengetyrotspoele in die somer bevolk by 'n liggaamsgrootte van 20–25 mm. Tot en met nege broeisels van eiers en embrio's van verskillende ouderdomme is terselfdertyd gevind in die gonade, alhoewel daar geen verhouding was tussen die getal broeisels en die visgrootte nie. Die totale aantal voortplantingselemente (eiers en embrio's) het egter toegeneem met vismassa in al die spesies. Voortplantingspotensiaal wat bereken is as die gemiddelde aantal broeisels per volwasse wyfie vermenigvuldig met die gemiddelde aantal voortplantingselemente per wyfie, het gewissel van 2843 in *C. acuminatus* (die hoogste syfer) tot 237 in *Muraenoclinus dorsalis*.

Fishes of the family Clinidae, locally known as klipfish, are endemic to southern Africa, occuring from Namibia to northern Natal. There are a total of 39 species in the family (Smith 1986), 25 of which have been collected in rotenone samples from the intertidal zone. Clinids dominate the intertidal ichthyofauna on the west and south-western coasts of southern Africa, constituting up to 98,5% of the total number of fish present (Prochazka & Griffiths 1992). Although the species composition of intertidal fish communities has been fairly intensively investigated at various sites around the South African coast (Marsh, Crowe & Siegfried 1978; Christensen & Winterbottom 1981; Bennett & Griffiths 1984; Beckley 1985a,b; Bennett 1987; Burger 1988, 1990; Prochazka & Griffiths 1992), few studies have investigated the biology of these species. Biological parameters that have been studied include the reproductive biology (Veith 1978, 1979, 1980) and energy budget (Bennett 1984) of *Clinus superciliosus*, and a study of the diets of the 16 most abundant clinid species in the south-western Cape (Bennett, Griffiths & Penrith 1983; Burger 1990).

Like all intertidal fish, the clinids face the danger of having their reproductive material transported to unfavourable offshore areas by wave action. Littoral fish have solved this problem in a number of ways, including attaching their eggs to the substratum and various forms of parental care (see Gibson 1982 for review). The southern African Clinidae exhibit the most extreme form of parental care, namely viviparity, the holding of eggs within the body until they hatch as fully developed young (Penrith 1970, Veith 1978, 1979, 1980).

Although viviparity reduces mortality during early development and ensures the retention of reproductive material within the intertidal zone, it involves energetic cost and reduces fecundity, resulting in a considerably smaller number of juveniles being produced by any one female (Wourms & Lombardi 1992). In an attempt to overcome this, the clinids have developed superembryonation, a state in which several broods of different ages develop within the ovaries at one time (Veith 1978, 1979). This means that adult females are capable of continuously supplying juveniles to the population and that breeding should occur throughout the year. This phenomenon has been previously noted for *Clinus superciliosus* (Veith 1979). The only other studies which have examined reproductive biology in South African clinids have dealt with embryonic and ovarian adaptations to viviparity in *C. super-*

ciliosus and *Muraenoclinus dorsalis* (Veith 1978, 1979, 1980; Cornish & Veith 1986; Veith & Cornish 1986; Cornish & Veith 1987). This paper thus aims to investigate the reproductive biology of intertidal clinids found commonly along the west coast of South Africa.

Methods

Fish were collected at monthly intervals from intertidal rock pools at Sea Point (33°55'S; 18°23'E) on the west coast of the Cape Peninsula between May 1992 and May 1993. Between 12 and 16 pools were sampled each month with the use of the ichthyocide rotenone. All comatose fish were caught using handnets and immediately placed in 70% ethanol. Care was taken to ensure that pools were not sampled more than once to avoid problems associated with recolonization. Fish were identified and separated into males, females and juveniles on the basis of external anatomy. This could be done easily as males possess a conspicuous intromittent organ. Only species which contributed more than 5% to the total catch and occurred in all months were considered further.

The ovaries were removed from all female fish of the six species mentioned above. They were weighed to four decimal places and the weight was expressed as a function of body mass from which monthly means were calculated. In addition, eggs and embryos present in the ovaries were measured and counted.

A sample of 200 males of each species was dissected and the development of the intromittent organ and testes noted. These data were used to determine size at 50% and 100% maturity for each species. Although all juveniles have a urogenital papilla, this becomes gradually enlarged to form the intromittent organ in males. Maturity was judged to have been attained only once the intromittent organ had reached its final form, which is unique in each species and has been described in detail by Penrith (1969). All mature males from each month were dissected and the weight of their testes expressed as a function of body mass to elucidate seasonal trends in gonad development.

Results and Discussion

A total of 5 409 fish belonging to 20 species and five families were collected from the 173 rockpools sampled. The family Clinidae contributed 92% to the total catch, the Gobiesocidae 8% and the Blenniidae, Gobiidae and Batrachoididae less than 1% each. The most abundant clinids were *C. superciliosus* (33%), *C. agilis* (16%), *M. dorsalis* (13%), *C. cottoides* (12%), *C. acuminatus* (10%) and *C. heterodon* (5%). In all species the smallest individuals caught measured 22–23 mm total length (Table 1), while the largest individuals recorded varied between 75 mm in *M. dorsalis* and 260 mm in *C. superciliosus* The sex ratio (Table 1) varied from 36% female in *C. acuminatus* to 53% female in *C. superciliosus*, although this was only significantly different from a 50:50 ratio in *C. acuminatus* (χ^2; $p < 0.05$). Why this occurs remains unknown, but it is interesting to note that Bennett (1983) reported a sex ratio of 94% female for *Clinus spatulatus* from the Bot River estuary.

Size at maturity

Size at both 50% and 100% maturity was larger for females than for males in all species considered (Figure 1), with the exception of *M. dorsalis*, in which females reached 100% maturity at 41–45 mm, while males reached this stage at between 46 and 50 mm total length. Size at 50% maturity varied between 35 and 85 mm in females and 25 and 60 mm in males. The size at maturity appeared to be related to maximum attainable size. Thus the smallest species, *M. dorsalis*, which attains only 75 mm, reached 50% maturity at 36–40 mm in females and 26–30mm in males. At the other extreme, males of *C. superciliosus*, which attain a maximum size of 30 cm, reached 50% maturity at 51–55 mm in length. Although 50% maturity for females of this species appeared to occur between 81 and 85 mm, this is an artefact of a low sample number in this size class (n =2), and size at 50% maturity is in reality only reached at 106–110 mm total length. This is in agreement with Veith (1978) who reported that the smallest gravid *C. superciliosus* found by him weighed 18,4 g, which would correspond to a total length of approximately 114 mm.

Breeding season

Maximum gonad mass varied in males from as little as 2,56% of body mass in *C. superciliosus* to as much as 11,56% in *M. dorsalis* (Table 2) and in females between 8,85% (*C. superciliosus*) and 27,85% (*C. agilis*). Average gonad mass of females was greatest in *M. dorsalis* (5,87%) and lowest in *C. superciliosus* (0,27%). Male *M. dorsalis* displayed the highest average gonad mass (4,92%) and *C. superciliosus* the lowest (1,03%). By contrast, Veith (1978) reported that average gonad mass contributed only 0,49% of total mass in male *C. superciliosus*, but this was based on a sample size of only six individuals. It is interesting to note that these values were greatest in those species that attain a relatively small maxi

Table 1 Size ranges and sex ratios of six species of clinid fish from intertidal pools at Sea Point

Species	N	Size range (mm)		Sex ratio	
		Min	Max	%F	%M
Clinus acuminatus	551	23	138	36	64
Clinus agilis	882	22	115	46	54
Clinus cottoides	631	22	130	46	54
Clinus heterodon	284	22	126	40	60
Clinus superciliosus	1798	23	260	53	47
Muraenoclinus dorsalis	709	22	75	50	50

Table 2 Average and maximum gonad mass as a percentage of total mass for males and females of six species of intertidal clinid fish

Species	Females		Males	
	Ave	Max	Ave	Max
Clinus acuminatus	1,76	18,84	1,57	4,31
Clinus agilis	4,72	27,85	3,81	7,76
Clinus cottoides	1,74	26,39	1,82	6,25
Clinus heterodon	0,90	14,97	1,78	4,97
Clinus superciliosus	0,27	8,85	1,03	2,56
Muraenoclinus dorsalis	5,87	20,53	4,92	11,56

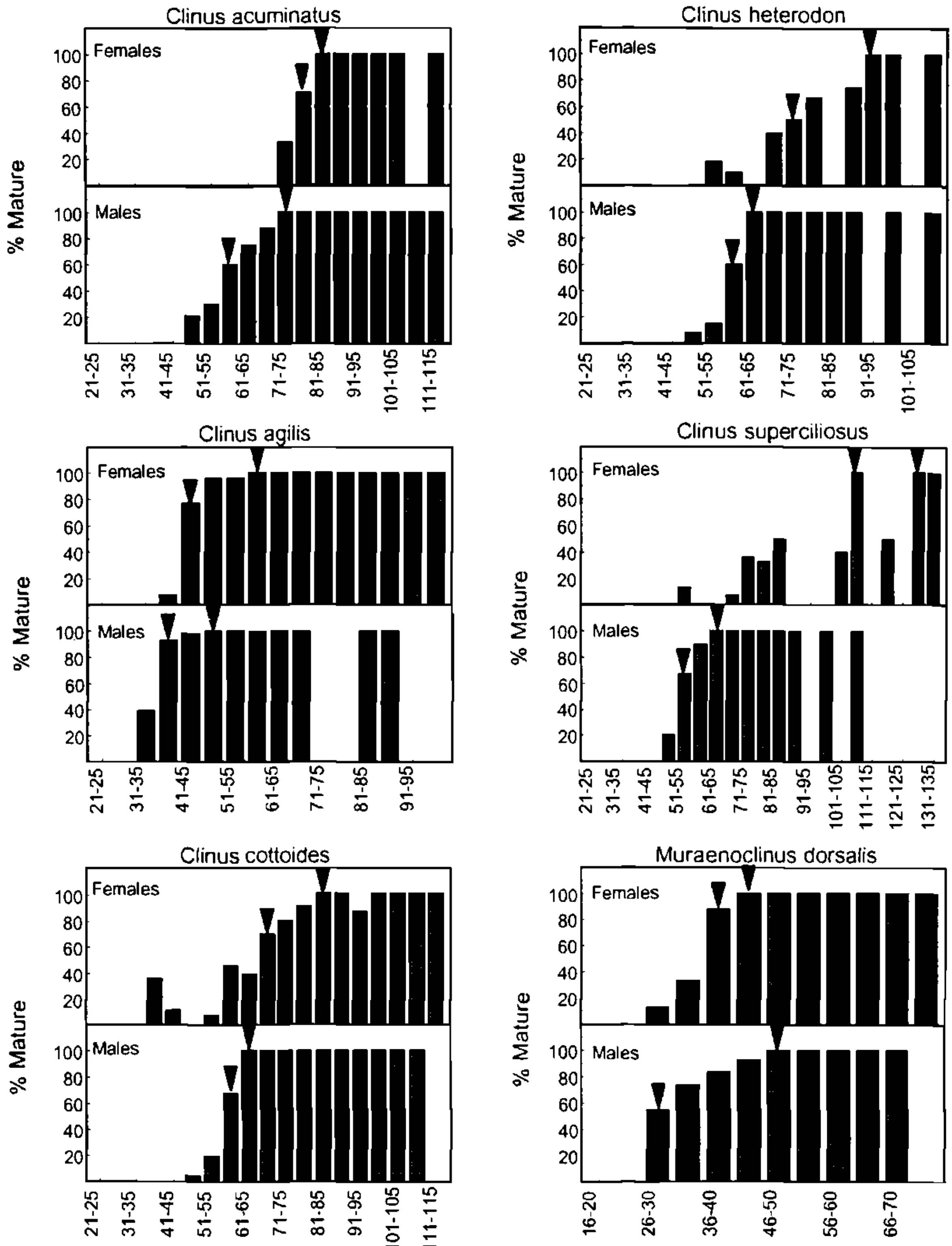

Figure 1 The percentage of mature individuals within 5 mm size classes for both females and males of six species of intertidal clinid fish. Arrows indicate the size classes within which 50% and 100% maturity were attained.

mum size (*C. agilis* and *M. dorsalis*) and lowest in the largest species (*C. superciliosus*). In general, larger organisms tend to have a greater longevity than smaller ones. Thus species which attain a large size may channel relatively less energy into each reproductive bout, but reproduce over longer time scales.

Seasonal changes in the relationship between gonad mass and total mass of mature fish are plotted in Figure 2. In all species peaks of male gonad development were followed by an increase in the relative gonad mass of females, as might be expected since insemination is required before embryo development commences. Males of *Clinus acuminatus*, *C. agilis*, *C. cottoides*, *C. heterodon* and *M. dorsalis* reached peak gonad mass in autumn (March to May), while in females of

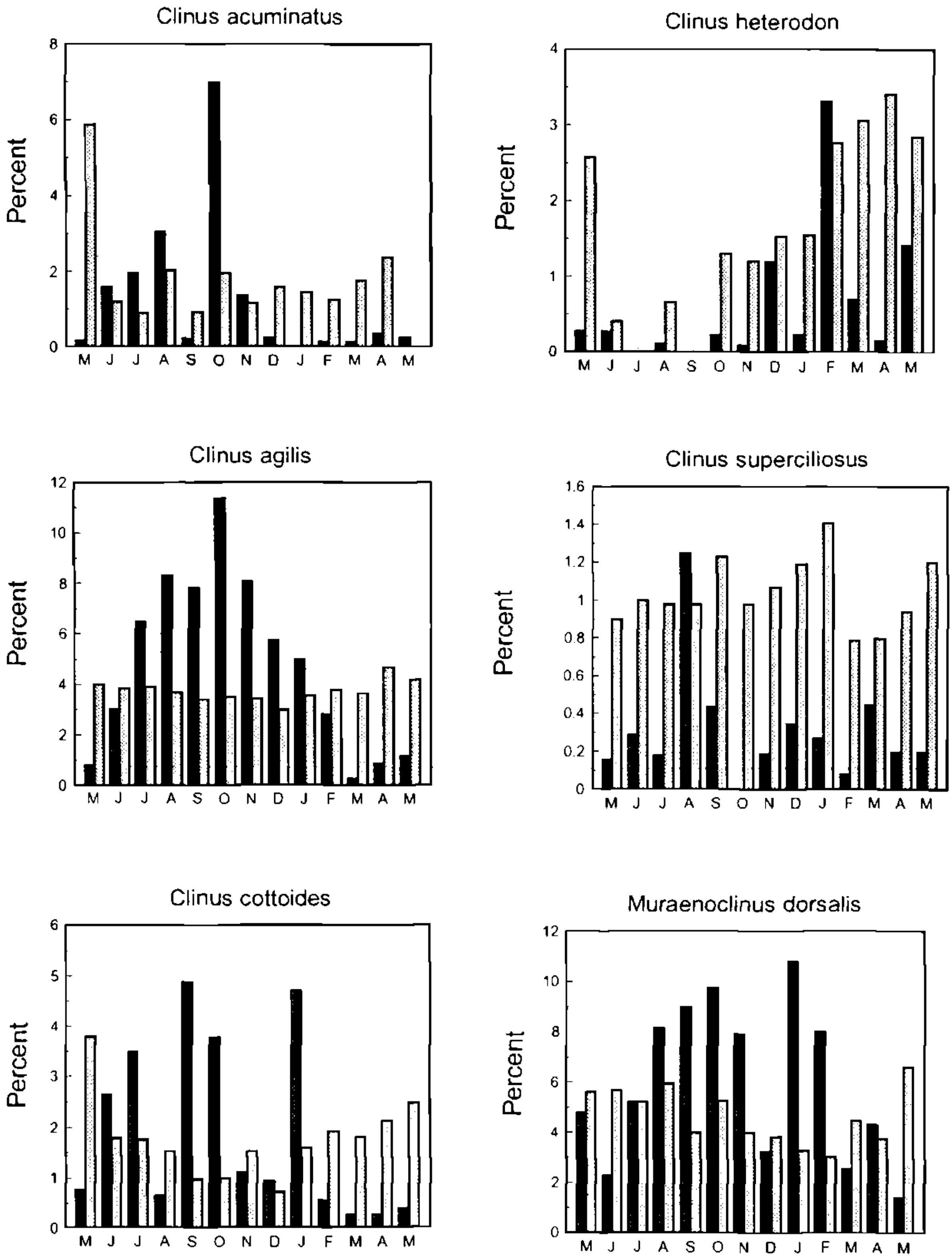

Figure 2 Gonad mass as a percentage of total body mass for females (dark shading) and males (light shading) of six species of intertidal clinids throughout the sampling period.

C. acuminatus and *C. agilis* gonad mass peaked in spring (September to November), and in *C. heterodon* in summer (December to February). In females of *C. cottoides* and *M. dorsalis* gonad mass peaked around September and October and then again in January. The time lag between the peaks in male and female gonad mass would suggest a gestation period between insemination and parturition of the most mature embryos of approximately 4–6 months. By comparison, viviparous teleosts of the genus *Sebastes* have been reported to have gestation periods of 1–2 months (Boehlert & Yoklavich 1984).

The only species which failed to show distinct seasonal trends in gonad mass of either males or females was *C. superciliosus*. There are two possible explanations for this. Either this species does breed throughout the year, as suggested by Penrith (1970) and Veith (1978, 1979), or the sampling program, which was confined to the intertidal zone, was biased towards collection of relatively small individuals of this species which had not reached their full reproductive potential.

Penrith (1970) stated that *C. acuminatus, C. cottoides* and *C. superciliosus* breed throughout the year. Although some reproductive activity may continue throughout the year, there appear to be seasonal peaks in reproductive activity in all species except *C. superciliosus*. These peaks appear timed so that females give birth in spring and summer, when elevated tide-pool temperatures are likely to enhance juvenile growth.

Recruitment

The smallest recruits captured measured between 22 and 23 mm in total length in all species sampled (Table 1). Figure 3 indicates the number of smallest recruits (21–25 mm size class) in each month throughout the sampling programme. Recruitment of juvenile *C. acuminatus, C. agilis* and *C. cottoides* occured in summer/autumn and appeared to follow shortly after the peak in female gonad mass, as might be expected. Juveniles of *C. heterodon* and *M. dorsalis*, however, started recruiting while female gonad mass was still on the increase, but before it had reached its peak. Smallest recruits of *C. superciliosus* were present only in February. Why recruitment should be so strongly pulsed in a species which reportedly breeds throughout the year (Veith 1978, 1989; Penrith 1970) remains unclear.

Number of broods

As shown by Veith (1979, 1980) clinid fishes may incubate several broods of eggs and embryos of different ages simultaneously. The average number of broods of different ages in the ovaries of mature females (Table 3) was lowest in *C. heterodon* (2,56) and highest in *M. dorsalis* (5,26), while the maximum number of broods varied between five in *C. heterodon* and nine in *M. dorsalis*. The maximim number of broods found in *C. superciliosus* during this study was seven, although Veith (1978) reported that up to 12 broods may be present in the ovaries at any one time. No relationship could be found between the number of broods and fish mass for any of the species studied.

Fecundity

The average number of reproductive elements (eggs and embryos) in the ovaries of the various clinid species ranged from 45 in *M. dorsalis* to 629 in *C. acuminatus* (Table 3). The maximum number of reproductive elements showed the same trend (126 in *M. dorsalis* to 1 896 in *C. acuminatus*). In all species the majority of the reproductive elements were eggs, with the average number of embryos ranging between 14 and 91 in *M. dorsalis* and *C. acuminatus* respectively. Egg numbers were low compared to those reported for rockfishes, which vary between 6 000 and 2,3 million eggs per female (Phillips 1964). The total number of reproductive elements appeared to increase with fish mass in all species (Figure 4), although significant regressions could be fitted only for *C. acuminatus* r^2 =80,18; $p < 0{,}001$) and *C. cottoides* (r^2 = 67,05; $p < 0{,}001$). This is consistent with the findings of Veith (1978, 1979) who reported a linear relationship between the number of embryos present in the ovaries and fish mass in *C. superciliosus*. Similar findings have been reported by workers studying other viviparous species (Phillips 1964).

Reproductive potential

Multiplying the average number of broods per mature female by the average number of reproductive elements gives an indication of reproductive potential for each species (Table 3). This was greatest in *C. acuminatus* (2 843), intermediate in *C. agilis* (529), *C. cottoides* (961), *C. heterodon* (574) and *C. superciliosus* (558), and lowest in *M. dorsalis* (237). Although this estimate may be inaccurate if not all the eggs present develop within the same season, it nevertheless serves as a between-species comparison of female reproductive investment. It is interesting to note that, although gonad mass made up the largest proportion of the body mass of the two smallest species (*C. agilis* and *M. dorsalis*), reproductive potential in these species remained lower than for all other species.

Size at birth

The maximum size of embryos in the ovaries (Table 3) suggests that juveniles are born at a total length of between 13 and 20 mm. This agrees with the findings of Veith (1978, 1979, 1980) who found that *C. superciliosus* embryos of 20 mm in length were fully developed and ready for birth.

Conclusions

Although previous workers have stated that the South African Clinidae breed throughout the year (Penrith 1970; Veith 1978,

Table 3 Number of broods per female, total reproductive elements, eggs and embryos, as well as reproductive potential and maximum embryo size (mm) of six species of intertidal clinid fish

Species	No. broods		No. elements		No. eggs		No. embryos		Reproductive potential	Maximum embryo size
	Ave	Max	Ave	Max	Ave	Max	Ave	Max		
Clinus acuminatus	4,52	7	629	1896	538	1428	91	468	2843	13
Clinus agilis	4,04	8	131	368	100	266	31	192	529	15
Clinus cottoides	3,03	7	317	1126	301	864	15	262	961	15
Clinus heterodon	2,56	5	330	1160	312	1018	18	142	574	13
Clinus superciliosus	2,63	7	212	850	191	706	20	144	558	20
Muraenoclinus dorsalis	5,26	9	45	126	31	105	14	40	237	20

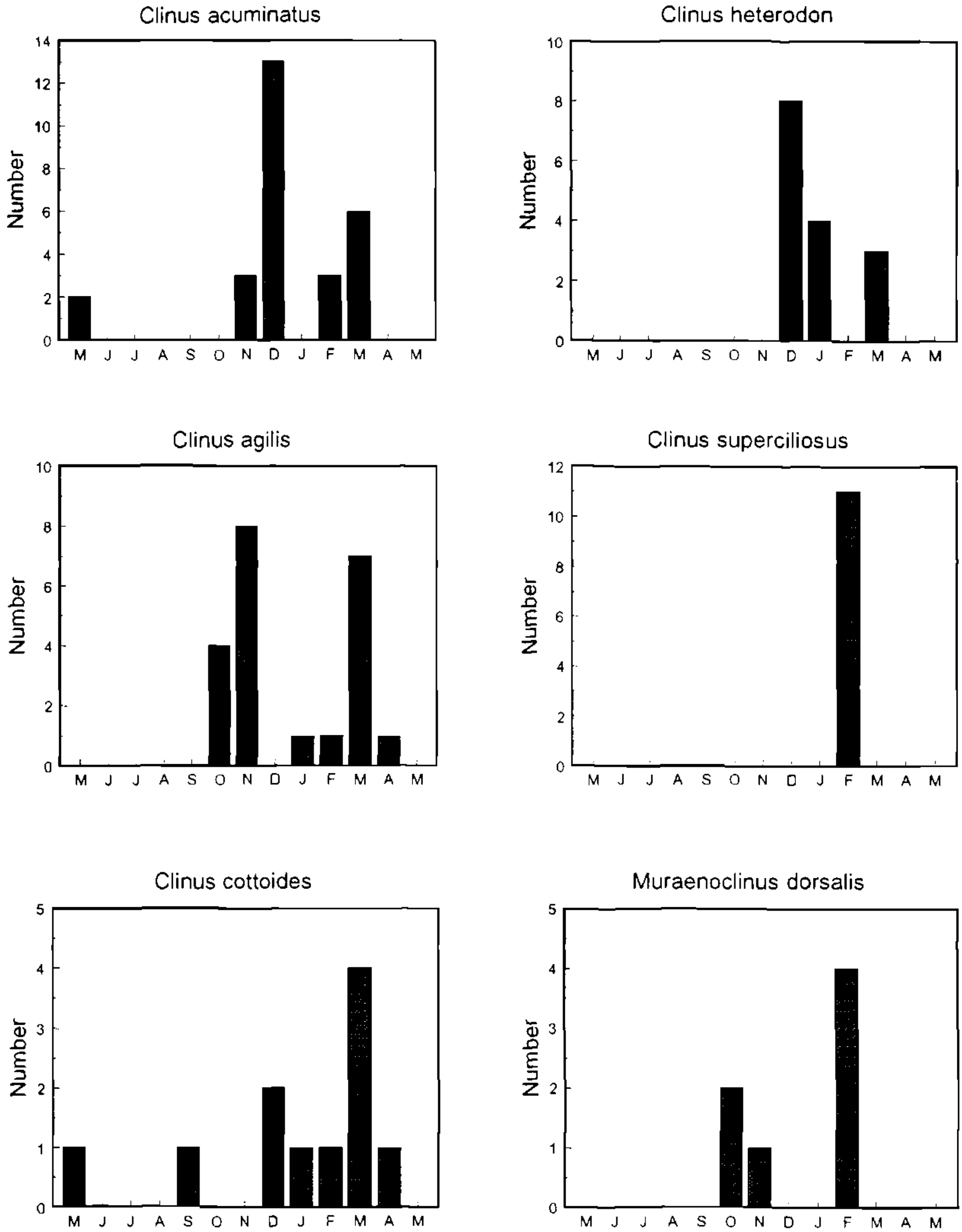

Figure 3 The number of smallest recruits (21–25 mm size class) of each of six species of intertidal clinids caught throughout the year.

1979), this study indicated that seasonal peaks in reproductive activity occur in five of the six species examined. Males reached a peak in gonad mass in autumn and winter. After a gestation period of 4–6 months this was followed by a peak in female gonad mass and subsequently recruitment of juveniles of approximately 20 mm total length into the population in summer and autumn. At this time of year tidepool temperatures are elevated (Huggett & Griffiths 1986), wave action is at a minimum and tidepools are covered in seasonal growth of green algae such as *Ulva* spp. (McQuaid, Branch & Crowe 1985), which provide cover for recruits (pers. obs.) as well as for numerous small prey organisms such as amphipods and isopods, which form the major prey types for all species of clinids (Bennett, Griffiths & Penrith 1983).

The exception to the above pattern is *C. superciliosus*, which has been reported to breed throughout the year (Penrith

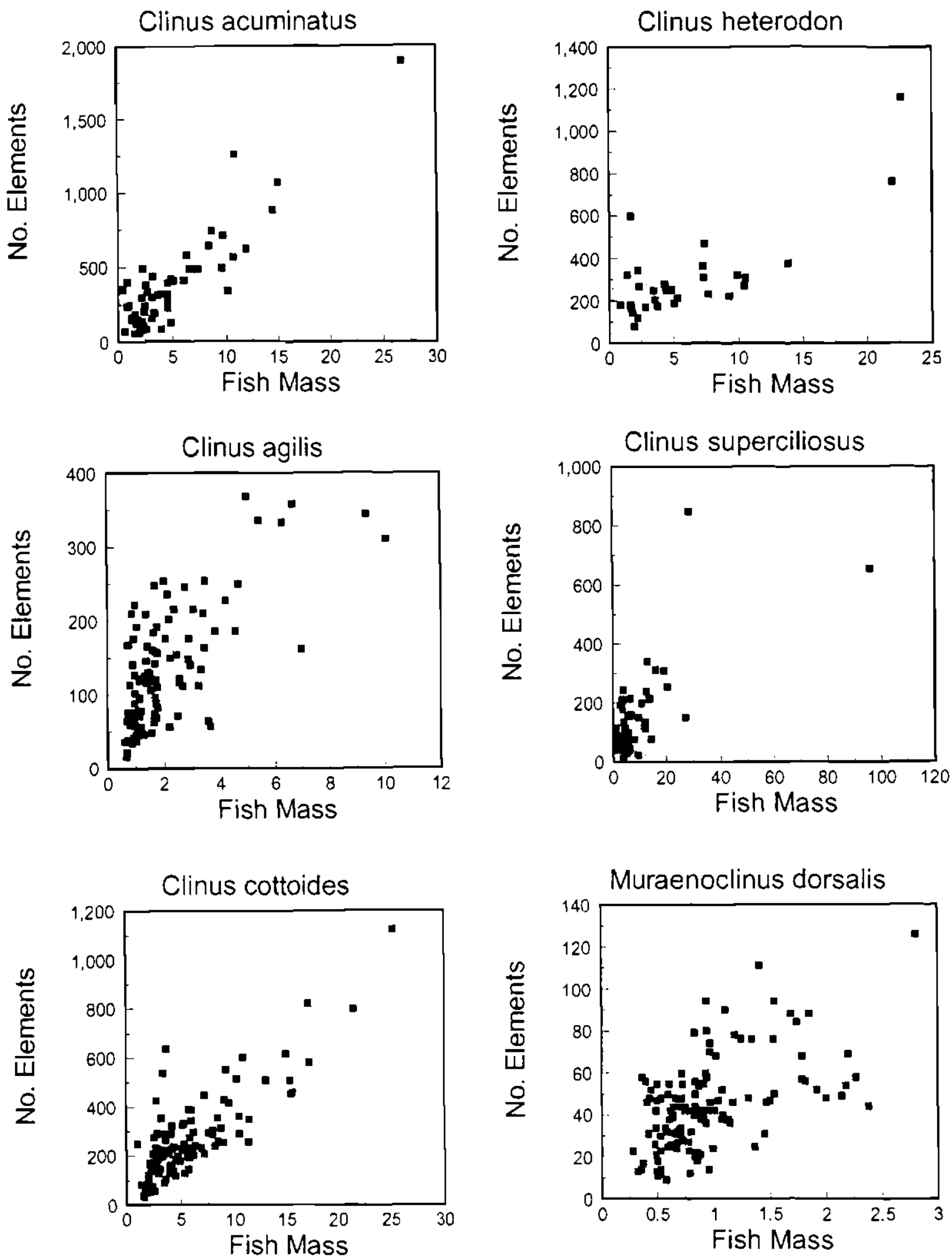

Figure 4 The total number or reproductive elements, including both eggs and embryos, as a function of total body mass for six species of intertidal clinids.

1970, Veith 1978, 1979). The present study found no seasonal increase in breeding activity, although smallest recruits were found to occur in February only. The reasons for recruitment being so markedly seasonal in a species which breeds all year round remain obscure.

While viviparity greatly enhances the survival of juvenile stages, it has certain restrictions, the most important of which is the reduced number of reproductive elements that a female can produce at any one time (Wourms & Lombardi 1992). Superembryonation enables fish to produce a greater number of embryos over a protracted period. It has been noted (Table 3) that the smaller the species, the fewer reproductive elements it has. This is particularly noticeable in *M. dorsalis*. Although the number of broods is greater in this species, its reproductive potential remains lower than for all the other species. It is assumed that the benefits accrued by the small size and slender body form of this species, which allows individuals to take refuge in very small crevices, outweigh the decrease in reproductive potential.

Acknowledgements

The author would like to thank hardy field assistants, especially Lesley Prochazka, Yves Lechanteur and Lisa Kruger. Charles Griffiths commented on the manuscript. This work was made possible in the earlier stages by a postgraduate bursary from the Foundation for Research Development and later by a Foundation for Research Development Core Programme Grant to G.M. Branch, J.G. Field and C.L. Griffiths.

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