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Consistent timing of juvenile fish recruitment to seagrass beds within two Sydney estuaries

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Abstract. Recruitment patterns of juvenile *Rhabdosargus sarba* (Sparidae) and *Pelates sexlineatus* (Terapontidae) were examined by frequent (1–4 weeks) beach seining of seagrass beds in Sydney, south-east Australia. Two sites within each of two estuaries (Botany Bay and Pitt Water) were sampled for one year. One site within Botany Bay was sampled for 3 years. A total of 12 824 juveniles of *R. sarba* and 7037 juveniles of *P. sexlineatus* were collected. *R. sarba* recruited in 4 pulses during winter/spring, while *P. sexlineatus* recruited in 6 pulses during summer/autumn, and the timing of recruitment events was consistent among locations and years. *P. sexlineatus* recruitment coincided with new moons, but *R. sarba* recruitment dates were less precisely determined. Predictable annual recruitment patterns result in temporal partitioning of seagrass habitat between these two abundant estuarine species. Spatial differences in magnitude of recruitment events among sites reflected patterns of estuarine circulation.

Extra keywords: tarwhine, six-lined trumpeter, *Zostera*, *Posidonia*

Introduction

Pelagic larvae recruiting to demersal habitats often do so in pulses, which can influence the structure of juvenile and adult populations (Roughgarden *et al.* 1988; Doherty and Fowler 1994). Larvae that rely on passive advection by stochastic oceanographic processes as a primary recruitment mechanism characteristically arrive in pulses that are irregular in timing, strength or location. These processes contribute to recruitment variability in a diversity of coastal habitats (Cowen 1985; Kingsford 1990; Milicich 1994; Jones and Epifanio 1995; Jenkins *et al.* 1997).

Alternatively, patterns of recruitment may reflect the timing and strength of spawning events (Robertson *et al.* 1988; Carr 1991), or may be synchronized with lunar or tidal cycles (e.g. Robertson 1992; Rothlisberg *et al.* 1995; Forward *et al.* 1998). Recent studies have recognized that the recruitment patterns of fish are frequently quite consistent and that the role of larval behaviour may be significant in the recruitment process (Thorrold *et al.* 1994a, 1994b; Sponaugle and Cowen 1997; Leis and Carson-Ewart 1998; Tolimieri *et al.* 1998). Regular or predictable patterns of recruitment are likely to reflect a reliance on highly predictable mechanisms, such as tidal currents and larval behaviour. Examination of large-scale or longer-term recruitment patterns may therefore provide an indication as to the nature of the recruitment process.

Information on the processes of estuarine recruitment by marine fish larvae along eastern Australia is scarce (but see State Pollution Control Commission (SPCC) 1981; Miskiewicz 1986; Bell *et al.* 1987; McNeill *et al.* 1992). Most previous studies have been conducted over periods of less than one year and with sampling frequencies of one month or more. The timing of recruitment at scales of days or weeks has been examined for only one species, *Acanthopagrus australis* (Pollock *et al.* 1983), and the degree of consistency in recruitment patterns at these scales among years is unknown for any species. Considerable potential exists for recruitment variability, arising from oceanographic variability, along the south-eastern Australian coast. In particular, the inner continental shelf is subject to frequent, but irregular, fluctuations in cross-shore and along-shore current direction and velocity (Middleton *et al.* 1997). These processes result in considerable temporal and spatial variability in the distribution of larval fish over the shelf (Smith and Suthers 1999; Smith *et al.* 1999), which may, potentially, contribute to variability in coastal recruitment.

The aims of this study were to investigate recruitment patterns of juvenile fish of two species common to south-eastern Australian seagrass beds, and to compare the timing of recruitment to tides, local winds, and estuarine circulation. *Rhabdosargus sarba* (Sparidae) and *Pelates sexlineatus* (Terapontidae) are members of the 10 most common fish

families occurring in Australian seagrass beds (Pollard 1984). Both species spawn outside estuaries, and juveniles are abundant in seagrass for several months after settlement.

Rhabdosargus sarba (Sparidae) occurs throughout temperate regions of the Indo-Pacific, including Australia's east and west coasts, Japan and the east coast of South Africa (Miskiewicz and Neira 1998). *Pelates sexlineatus* (Terapontidae) is distributed along the south-east coast of Australia (Trnski and Neira 1998). Distributional records are confused with that of *P. quadrilineatus*, which occurs on northern Australian coasts, and with *P. octolineatus*, which occurs along the south-west coast. *R. sarba* and *P. sexlineatus* juveniles are very abundant within estuaries on the east coast of Australia, and adults occur in shallow shelf waters. Both species are caught by commercial and recreational fishers. Spawning by either species has not been observed but probably occurs outside estuaries, as suggested by (i) a seasonal abundance of larvae in shelf waters, (ii) a rarity of young larvae within estuaries, and (iii) a relatively high abundance of older larvae and young juveniles at estuarine sites, especially those sites close to the ocean (Wallace 1975; Young 1981; Bell and Westoby 1986; Miskiewicz 1986; Loneragan et al. 1986; Gray 1995; Hannan and Williams 1998; Smith and Suthers 1999). *P. sexlineatus* may spawn near estuary entrances whereas *R. sarba* spawns in coastal waters not adjacent to estuaries (Wallace 1975; Miskiewicz 1986; Hyndes et al. 1999).

In south-east Australian continental shelf waters, larvae of both species occur throughout the year, suggesting a highly protracted spawning season. Recently settled juveniles of *Rhabdosargus sarba* and *Pelates* spp. have been observed from May to December, and November to June, respectively (reviewed by Smith 1999). Age at settlement is unknown, but length at settlement is ~10 mm for each species (Miskiewicz and Neira 1998; Trnski and Neira 1998). Larvae may recruit to the first appropriate seagrass habitat encountered (irrespective of leaf height/density), with migration to seagrass beds upstream of initial recruitment occurring several weeks/months after settlement (Bell and Westoby 1986; Loneragan et al. 1986; Bell et al. 1987; Hannan and Williams 1998). Juveniles remain in estuaries for at least 1 year after settlement (SPCC 1981; Potter et al. 1983; Hannan and Williams 1998).

Methods

Sampling sites

Botany Bay and Pitt Water are tidal embayments ~50 km apart (Fig. 1). Maximum depth in each estuary is 20 m, although depth is mostly <5 m. Benthic habitats within both estuaries are predominantly seagrass or bare sand. Mangroves occur along the southern shores and rocky reef and kelp beds occur at the heads. Pitt Water is an arm of the Hawkesbury River but receives little freshwater input from it, and so salinity gradients are weak. Botany Bay receives freshwater from the Georges and Cooks Rivers. The Georges River is the larger of the two, with flow rates generally <5 m³ s⁻¹. Tidal exchange in Botany Bay exceeds 4000 m³ s⁻¹ (SPCC 1979). Tidal currents in each estuary are generally <0.5 m s⁻¹ (SPCC 1979; Cox et al. 1993). The northern side of Botany Bay has been greatly altered by the construction of a port and airport. Pitt Water

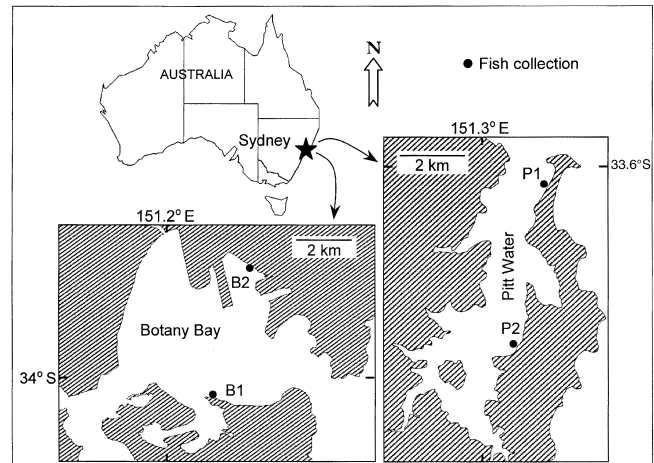


Fig. 1. Location of sampling sites B1 and B2 within Botany Bay, and sites P1 and P2 within Pitt Water.

is less developed, with residential development to the east and national park to the west.

Four sites were sampled (Fig. 1). Sites B1 and B2 were ~4 and ~6 km from the entrance of Botany Bay, on the southern and northern shores, respectively. Sites P1 and P2 were both on the eastern shore of Pitt Water, ~2 and ~6 km from the entrance, respectively. *Posidonia australis* was the dominant species of seagrass at B1 and P1, although a small amount of *Zostera capricorni* grew adjacent to the beach at each site. B2 contained monospecific beds of *Z. capricorni*, and P2 contained predominantly *Z. capricorni* with some *P. australis* and *Halophila ovalis*. Beds were interspersed with areas of bare sand at B2 whereas seagrass cover was relatively uniform at other sites.

Data collection

Juvenile fish at all sites were sampled approximately fortnightly from August 1995 to July 1996. Site B2 was also sampled for 6 months prior to and 16 months after this time (February 1995 to November 1997). Prior to 20 September 1995, samples were collected by a 40 × 2 m beach-seine net of 12 mm mesh. After this date, samples were collected by a 20 × 2 m beach-seine net of 6 mm mesh. An independent comparison of *Rhabdosargus sarba* (hereinafter *Rhabdosargus*) catches from two hauls by each net, conducted on the same day at B2, found that the large-mesh net retained no individuals <11 mm in length and fewer individuals 11–16 mm than the small-mesh net (2% of individuals were <1 mm in small mesh; 71/43% of individuals in small/large mesh were 11–16 mm).

Two to four replicate hauls were taken at each site on each sampling occasion. Individual hauls covered an area of ~200 m² and areas sampled by replicate hauls were separated by at least 5 m. Sampling was completed within 2 h of low tide. Where possible, sites within estuaries were sampled on the same day and estuaries were sampled on consecutive days. Individuals of *Rhabdosargus* and *Pelates sexlineatus* (hereafter *Pelates*) were retained and counted. The standard lengths of individuals were measured to the nearest 0.1 mm by image analysis.

Analysis

Replicate samples were pooled to calculate length-frequencies for each sampling occasion at each site. Individuals of *Rhabdosargus* and *Pelates* were grouped into 1 and 2 mm length classes, respectively. A series of normal distributions ('cohorts') were fitted to length frequencies using the 'MIX' computer program (McDonald and Pitcher 1979). The MIX output included mean length, standard deviation, and proportion that each cohort contributed to total sample abundance. A *P*-value indicating goodness of the overall fit for each sample was calculated (*P* = 1.0 indicates a perfect

fit). Total annual abundances of species or cohorts were calculated by summing all individuals in samples each year.

Results

Rhabdosargus sarba

Between February and September 1995, B2 was sampled with a 12 mm mesh net. Samples of *Rhabdosargus* collected with this mesh contained no individuals <11 mm in length

(Fig. 2). From September 1995 to July 1996, 6 mm mesh was used at all sites. *Rhabdosargus* was most abundant at B2 during this period (averaging 5.38 juveniles per 10 m²) (Fig. 2). Fewer juveniles were caught at B1 (0.28 per 10 m²), and very few occurred at P1 and P2 (0.01 per 10 m² at each site) (Fig. 3). Between August 1996 and November 1997, sampling with 6 mm mesh continued at B2, where abundances were again relatively high (averaging 7.10 individuals per 10 m²) (Fig. 2).

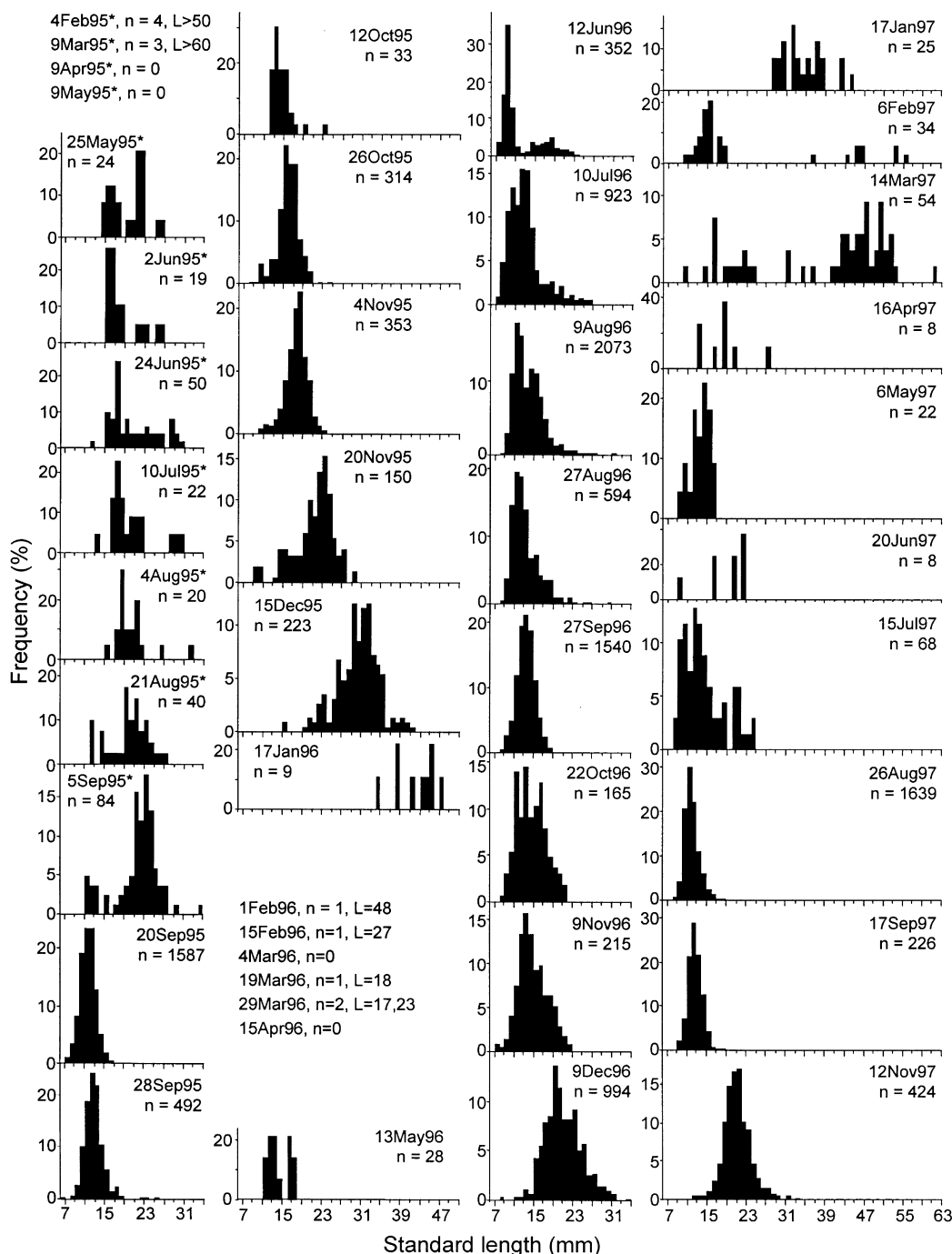


Fig. 2. *Rhabdosargus* length frequencies by sampling date at site B2, February 1995 to November 1997. (*, sampled by 12 mm mesh net; L, standard length; n, number of individuals)

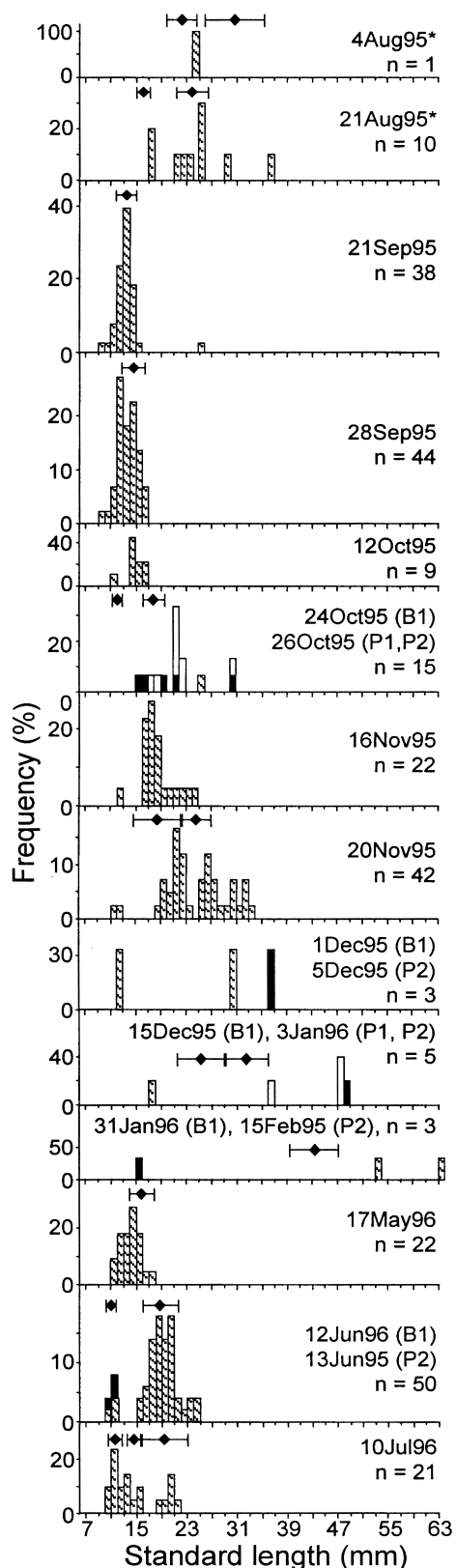


Fig. 3. *Rhabdosargus* length frequencies by sampling date at site B1 (hatched), P1 (white) and P2 (black), August 1995 to July 1996. Mean length (\pm sd) of cohorts from adjacent sampling times at site B2 superimposed over histograms. (*, sampled by 12 mm mesh net; n, number of individuals)

At B2 the occurrence of small (<15 mm) *Rhabdosargus* was seasonal (May–November 1995, May–December 1996, and February–November 1997), and *Rhabdosargus* length frequencies identified four cohorts of new recruits within the recruitment season each year (Table 1, Fig. 4). Low abundances prevented analysis of length frequencies at sites other than B2. However, a comparison of length frequencies at B1, P1 and P2 with mean lengths (\pm s.d.) of cohorts identified at B2 during adjacent sampling times indicated that the population size structure was similar among sites (Fig. 3). This suggested that cohort recruitment to B1, P1 and P2 was weaker in abundance but similar in timing to that which occurred at B2.

Mean length of all cohorts against day of year, irrespective of year number, suggested five periods of potential *Rhabdosargus* recruitment at B2 per year (February, May, June, July and October), which were consistent in timing among years (Fig. 4). Four of the five potential cohorts were observed within each year. There was no cohort associated with June 1995, February 1996, or October 1997.

Relative abundances of *Rhabdosargus* cohorts in samples were similar among years (Fig. 5a). July recruits contributed most to total annual abundance (92% in 1995, 54% in 1996, 69% in 1997), followed by June (0%, 29%, 27%). In 1995, abundances of February, May and June cohorts were probably underestimated, and July and October cohorts overestimated, because of the larger mesh size employed until September of that year.

Using similar methods to analyse length frequency data of *Rhabdosargus*, Worthington *et al.* (1992) described two cohorts at B2 that match closely in timing and fish length to the May and June cohorts identified in this study. For example, they described two cohorts on 24 July 1990 with mean fork lengths of 22.08 ± 2.67 mm and 15.17 ± 1.23 mm, respectively, which is in close agreement with the mean standard lengths of May and June cohorts during July 1995–97 (Table 1, Fig. 4). Low sampling frequency (8 times in 12 months) may partly explain why no other cohorts were observed by Worthington *et al.* (1992).

Pelates sexlineatus

Pelates was present at all sites between November 1995 and July 1996 (Figs 6 and 7). Abundances were highest at P2 (averaging 3.92 individuals per 10 m²), followed by B2 (3.02 per 10 m²), P1 (1.48 per 10 m²) and B1 (0.43 per 10 m²). Between August 1996 and November 1997, sampling continued at B2, and abundances averaged 3.14 individuals per 10 m² (Fig. 6).

In Botany Bay, the frequency and abundance of small (<13 mm) *Pelates* was similar among sites (Fig. 6). Between November 1995 and July 1996, small individuals represented $9.6 \pm 13.3\%$ (mean \pm s.d.) of *Pelates* in samples at B1, and $10.2 \pm 25.1\%$ at B2. At B2 in 1996/97, small *Pelates* occurred during fewer months than in 1995/96. In particular, no small *Pelates* occurred at B2 in December 1996 or January 1997.

In Pitt Water, small *Pelates* occurred more frequently and more abundantly at P2 than P1 (Fig. 7). Between November

Table 1. Length of *Rhabdosargus* in cohorts recruiting to site B2, 1995–97
P, probability of normal distributions fitted by MIX where *P* = 1 indicates perfect fit; –, insufficient data to resolve cohorts

Date	Cohort length (mm)										<i>P</i>
	February		May		June		July		October		
	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.	
2 Jun 95 ^A	25.85	1.90	18.57	0.99							0.37
24 Jun 95 ^A	27.25	3.25	19.33	1.66							0.06
10 Jul 95 ^A	31.50	0.76	20.66	2.28							0.61
4 Aug 95 ^A	30.45	4.88	21.90	2.39							0.22
21 Aug 95 ^A	–	–	23.55	2.53			15.60	1.17			0.20
5 Sep 95 ^A			24.22	2.66			13.61	1.63			0.07
20 Sep 95			–	–			12.77	1.66			0.00
28 Sep 95							13.88	1.95	–	–	0.00
26 Oct 95							17.32	1.84	11.59	0.81	0.00
4 Nov 95							18.96	1.85	12.94	1.30	0.84
20 Nov 95							24.15	2.38	17.76	3.90	0.02
15 Dec 95							32.24	3.49	24.83	3.82	0.02
17 Jan 96							43.17	3.99	–	–	0.22
1 Feb 96							–	–			–
15 Apr 96			–	–							–
13 May 96			15.29	2.09	–	–					0.06
12 Jun 96			18.29	2.79	10.40	0.82	–	–			0.54
10 Jul 96			18.98	3.81	14.05	1.18	11.00	1.02			0.15
9 Aug 96			20.28	4.20	16.13	1.64	12.56	1.03			0.10
27 Aug 96			21.35	4.11	16.28	2.21	12.79	1.22			0.07
27 Sep 96			–	–	–	–	14.51	1.89	–	–	0.20
22 Oct 96							17.01	2.50	12.92	1.37	0.40
9 Nov 96							19.82	1.74	14.75	2.12	0.83
9 Dec 96							22.90	4.00	20.10	2.01	0.00
17 Jan 97	–	–					37.94	3.87	31.86	1.75	0.07
6 Feb 97	15.90	1.96					–	–	–	–	0.57
14 Mar 97	20.13	4.17							47.41	5.75	0.29
16 Apr 97	–	–	–	–					–	–	–
6 May 97			14.64	1.89							0.61
20 Jun 97			–	–	–	–	–	–			–
15 Jul 97			21.77	2.24	14.15	1.89	10.83	0.67			0.32
26 Aug 97			–	–	14.25	1.77	12.46	0.96			0.10
17 Sep 97					–	–	13.77	1.45			0.40
12 Nov 97					29.16	2.93	22.78	2.39			0.24

^A sampled by 12 mm mesh.

1995 and July 1996, individuals <13 mm represented 21.0 ± 15.1% (mean ± s.d.) of *Pelates* in samples at P2, but only 0.9 ± 2.5% at P1. Differences in the abundance of individuals <11 mm in length were even more marked – only 1 at P1, but 100 at P2.

Pelates length frequencies at P2, P1 and B2 indicated up to six cohorts of new recruits per site in 1995/96 (Table 2, Fig. 8a). Length frequencies at B1 could not be analysed because of low abundances. Cohort mean lengths against date suggested that cohorts recruited at similar times among sites (Fig. 8a), and so length frequencies from all sites in 1995/96 were pooled and mean lengths of the resultant cohorts plotted against day of year (Fig. 8b). Mean lengths of cohorts at B2 in 1996/97 were superimposed over these 1995/96 growth trajectories (Table 2, Fig. 8b). Sampling frequency was once per month in 1996/97, and so estimates of cohort growth may be

less accurate than in 1995/96 when sampling was twice per month. Three cohorts were observed to recruit in 1997. Initial mean lengths of these cohorts suggest that they recruited at similar times of year to three cohorts in 1996 (Fig. 8b). No recruitment was detected during November or December 1996, unlike in 1995.

Cohort recruitment dates in 1995/96 were estimated by extrapolating the initial section of each growth trajectory back to 10 mm, to approximate length at settlement (Fig. 8b). Recruitment was estimated to have occurred on 22 November, 22 December, 23 January, 17 February and 18 March, which was within 1, 0, 3, 2 and 1 days, respectively, of a new moon (Fig. 8b). The recruitment date of the final cohort in Pitt Water (observed May and June) was not evident from limited data, but was assumed to have occurred in April. Relative contributions of cohorts to total annual abundance of *Pelates* were

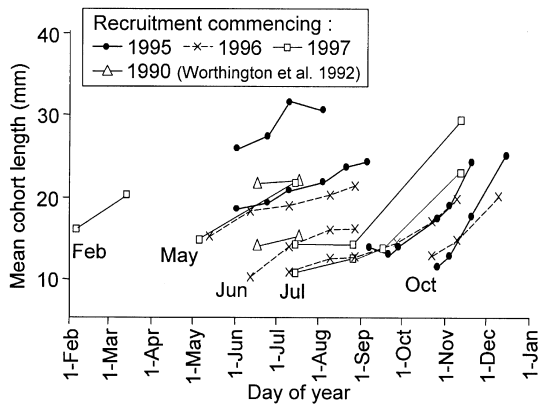


Fig. 4. Mean length of *Rhabdosargus* cohorts at site B2 against day of year, 1995 to 1997. Standard deviations omitted for clarity, but see Table 1 for values. Cohorts observed in 1990 at B2 by Worthington *et al.* (1992) included.

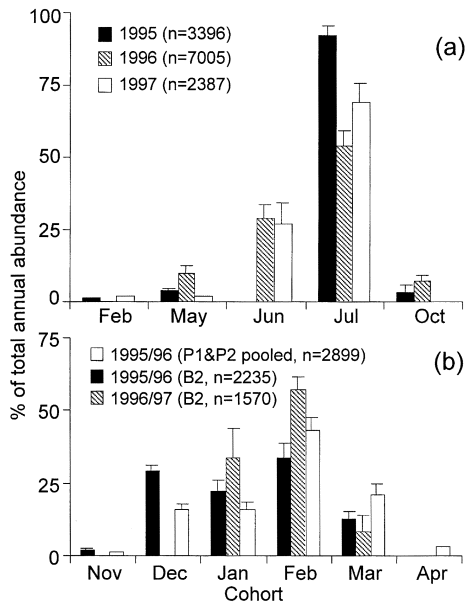


Fig. 5. Contribution by cohorts to total annual (a) *Rhabdosargus* abundance at site B2, 1995-97 and (b) *Pelates* abundance in Pitt Water (sites pooled), 1995/96, and at site B2, 1995/96 and 1996/97.

similar between the two estuaries and, at B2, among years (Fig. 5b). Generally, February recruits were most abundant, and November and April recruits were least abundant.

Discussion

Temporal patterns of recruitment

Rhabdosargus and *Pelates* recruited to Botany Bay and Pitt Water in four and six pulses, respectively, per year. The timing of these events was relatively consistent between estuaries and, at site B2, among years. This consistency suggests that processes influencing recruitment occur at scales of at least 50

km and may be predictable among years. These processes are likely to include advection by flood tides and larval behaviour.

Very slow initial growth rates during winter precluded accurate estimation of recruitment dates for *Rhabdosargus* cohorts; backwards extrapolation of growth trajectories of slow-growing cohorts was inappropriate because of the disproportionate effects of slight variations in slope of the growth curve. In contrast, growth rates of *Pelates* cohorts were higher and this technique was more successfully applied. Sampling at intervals of one week or less would be more appropriate for determination of recruitment times in *Rhabdosargus*. Estimates of recruitment times given here may allow future sampling effort to be more economically directed to achieve this.

Timing of *Pelates* recruitment was associated with new moons, suggesting that larvae employ tidal currents during recruitment to estuaries. High densities of post-flexion *Pelates* spp. larvae have been observed within coastal sewage plume fronts, suggesting a potential to also accumulate in estuarine fronts (Gray 1996). The time of entry by *Rhabdosargus* was not clear in this study, but post-larval *Rhabdosargus* enter Western Australian estuaries during flood tides (Neira and Potter 1992), and tidal stream transport is known from other sparids (Pollock *et al.* 1983; Whitfield 1989; Forward *et al.* 1998). New or full moons may represent a behavioural cue to larvae, or peak flood tides may increase the number of passively drifting larvae entering estuaries.

Lunar phase may also represent a spawning cue to adults, and the timing and number of recruitment events may partially reflect spawning activity. However, the limited number of recruitment events, despite the presence of *Pelates* and *Rhabdosargus* larvae in ocean waters throughout the year, suggests that recruitment in these species is not limited solely by spawning times, nor by tides and behaviour.

An advective force such as seasonal, coastal winds may also influence the onset of recruitment each year. *Rhabdosargus* recruitment commenced in May, peaked in July, and ceased in October. Each year, south-westerly winds were dominant between April and August, particularly in June and July. Hence, *Rhabdosargus* recruitment may have been associated with winds from this direction. At other times of the year, when *Pelates* recruited, winds were predominantly from the northeast or southeast. These two species may rely on different advective ocean processes for the coastal retention of early stage larvae or the transport of post-larvae to estuaries. Contrasting recruitment mechanisms may explain the temporal partitioning of juvenile habitat between these species.

The relative magnitude of recruitment pulses within years tended to be similar among years. Each year, the most abundant *Rhabdosargus* and *Pelates* cohorts were those recruiting in the middle of their respective recruitment seasons. Such patterns may reflect trends in spawning activity, which may peak at the centre of the spawning season (Wallace 1975; Miskiewicz 1986).

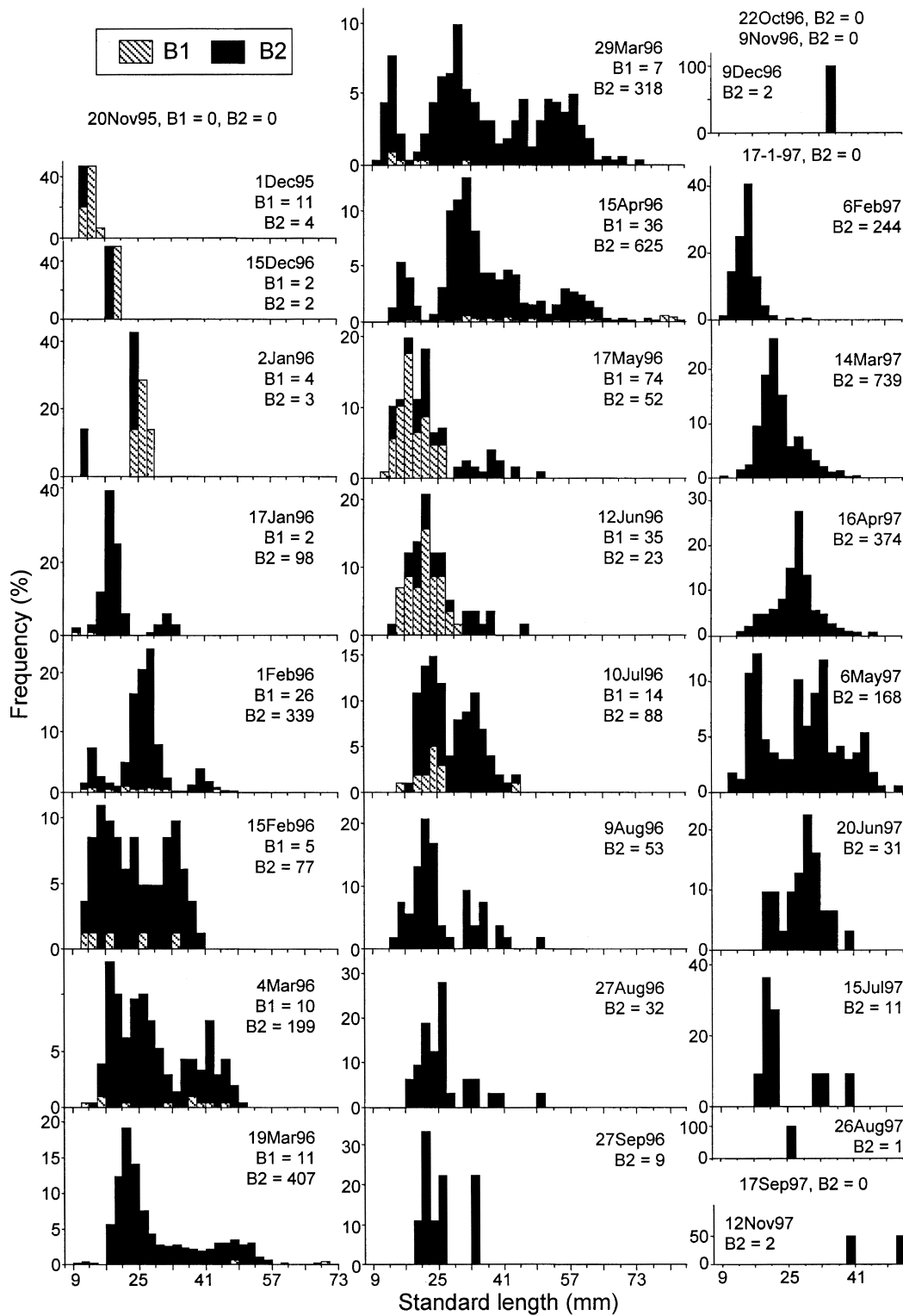


Fig. 6. *Pelates* length frequencies by sampling date at sites B1 (November 1995 to July 1996) and B2 (November 1995 to November 1997). (B1, abundance at site B1; B2, abundance at site B2)

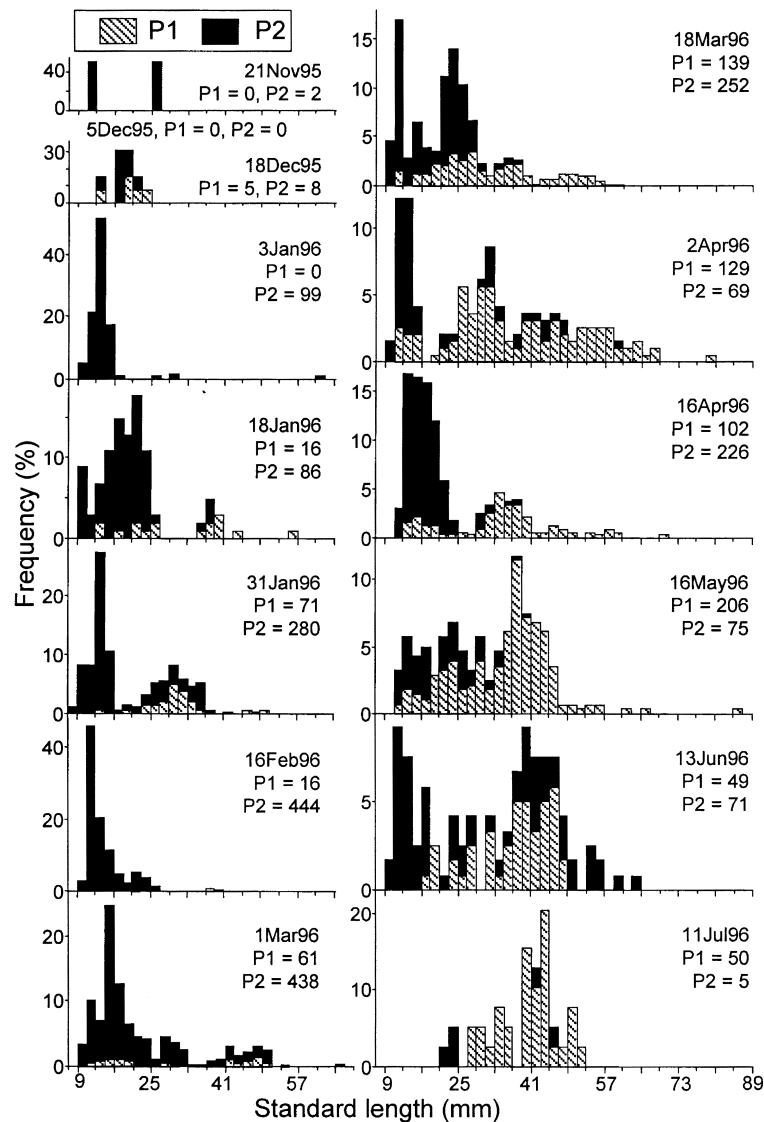


Fig. 7. *Pelates* length frequencies by sampling date at sites P1 and P2, November 1995 to July 1996. (P1, abundance at site P1; P2, abundance at site P2)

There was an apparent failure of *Rhabdosargus* cohorts to recruit in June 1995, February 1996 and October 1997. A cohort may actually have recruited in February 1996, albeit weakly, as evidenced by a small number of 15-25 mm individuals in February and March 1996. Other 'absences' coincided with sampling errors. Specifically, the use of 12 mm mesh precluded sampling of recently settled individuals in June 1995. In October 1997, a recruitment event may have gone unnoticed because no sample was taken during this month. The fact that these cohorts were not detected in subsequent samples may have been due to merging with older cohorts.

In contrast, the absence of *Pelates* recruitment in November and December 1996 was probably real and not due to sampling error. Large numbers of *Rhabdosargus* in samples at these times suggested that the net was operating

efficiently and so it is likely that *Pelates* recruitment did not commence until January 1997. Variations in spawning patterns or planktonic processes may have been responsible for the absence of *Pelates* cohorts in November and December of 1996/97.

Relative consistency in the timing and magnitude of annual recruitment may not only reflect predictable larval advection and behaviour, but may also reflect the stability of the nearshore pelagic environment from which these larvae recruit. Compared with much of the ocean, the nearshore zone is well mixed, has a relatively consistent plankton biomass, lower averaged along-shore drift and a tendency for cross-shelf retention (Smith *et al.* 1999). Thus, this region presents a 'stable' pelagic environment distinct from that overlying most of the continental shelf. Larvae that occur in

Table 2. Length of *Pelates* in cohorts recruiting to sites P1 and P2, 1995/96, and to site B2, 1995/96–96/97

P, probability of normal distributions fitted by MIX, where *P* = 1 indicates perfect fit; –, no sample taken, or insufficient data to resolve cohorts. Data from B1 not analysed because of insufficient data

Date	Site	Cohort length (mm)										<i>P</i>			
		November		December		January		February		March			April		
		Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.		Mean	s.d.	
18 Dec 95	P1	20.00	3.30	–	–										0.30
	P2	18.50	2.10	–	–										0.32
3 Jan 96	P1	–	–	–	–										–
	P2	28.66	1.79	13.75	1.49										0.41
17 Jan 96	B2	31.69	1.63	18.40	1.88										0.07
18 Jan 96	P1	39.43	2.25	20.77	4.57	–	–								0.24
	P2	37.38	0.08	19.66	3.02	–	–								0.21
31 Jan 96	P1	47.03	2.69	30.98	2.19	23.98	5.48								0.41
	P2	–	–	30.03	4.68	13.39	1.99								0.00
1 Feb 96	B2	40.32	1.87	26.50	2.38	14.65	1.43								0.27
15 Feb 96	B2	–	–	33.08	3.36	19.14	4.10								0.80
16 Feb 96	P1	–	–	38.92	4.09	19.69	4.36	–	–						0.12
	P2	–	–	–	–	–	–	–	–						–
1 Mar 96	P1	–	–	45.50	3.76	28.56	3.51	16.60	3.23						0.66
	P2	–	–	44.96	3.71	27.23	3.70	15.89	2.90						0.00
4 Mar 96	B2	–	–	41.13	4.27	25.82	3.30	18.50	1.45	–	–				0.55
18 Mar 96	P1	–	–	50.06	4.56	37.01	1.87	24.30	6.21	–	–				0.48
	P2	–	–	–	–	35.16	1.78	23.98	2.54	12.78	2.05				0.00
19 Mar 96	B2	–	–	48.07	4.11	31.21	7.06	22.18	2.35	–	–				0.37
29 Mar 96	B2	–	–	–	–	–	–	–	–	13.71	1.42				0.94
2 Apr 96	P1	–	–	54.52	6.87	42.12	2.84	29.41	3.87	13.84	1.55				0.93
	P2	–	–	–	–	–	–	–	–	13.09	1.37				0.94
15 Apr 96	B2	70.99	3.15	58.14	3.77	40.49	5.07	30.58	2.74	16.89	1.55				0.44
16 Apr 96	P1	–	–	56.95	5.71	46.94	1.64	35.36	3.86	17.14	2.54				0.30
	P2	–	–	–	–	–	–	32.16	3.25	17.14	2.85				0.00
13 May 96	B2	–	–	–	–	–	–	36.90	5.49	20.12	3.67	–	–		0.00
16 May 96	P1	–	–	–	–	53.70	6.72	39.56	4.01	24.30	4.76	14.06	1.24		0.27
	P2	–	–	–	–	–	–	–	–	25.73	5.56	14.96	2.07		0.01
12 Jun 96	B2	–	–	–	–	–	–	34.66	5.46	21.12	3.25	–	–		0.48
13 Jun 96	P1	–	–	–	–	–	–	41.97	3.70	27.70	6.18	–	–		0.06
	P2	–	–	–	–	54.44	5.12	41.63	4.48	25.27	1.93	14.02	2.39		0.15
10 Jul 96	B2	–	–	–	–	–	–	32.95	4.28	22.61	2.17	–	–		0.92
9 Aug 96	B2	–	–	–	–	–	–	35.05	5.77	21.13	2.98	–	–		0.08
27 Aug 96	B2	–	–	–	–	–	–	34.34	7.59	23.40	2.80	–	–		0.14
Sept 1996 to Jan 1997 – no <i>P. sexlineatus</i> in samples															
6 Feb 97	B2	–	–	–	–	15.44	2.44	–	–	–	–	–	–		0.00
14 Mar 97	B2	–	–	–	–	25.69	5.98	21.26	1.99	–	–	–	–		0.01
16 Apr 97	B2	–	–	–	–	29.65	6.10	27.89	1.40	20.64	3.32	–	–		0.15
6 May 97	B2	–	–	–	–	43.19	3.12	31.30	4.29	17.50	2.29	–	–		0.05

regions further offshore tend to exhibit considerable fluctuations in distribution, reflecting the variability of their environment. The degree to which larval distributions extend beyond the nearshore region may account for contrasting levels of variability in coastal fish recruitment.

Spatial patterns of recruitment

The distribution of recruitment observed in this study reflected patterns of estuarine circulation. Abundances at B2 during this study were consistently higher than at the other sampling locations. The northern shore of Botany Bay, in the region of B2, has previously been noted to exhibit “outstanding” levels of recruitment (McNeill *et al.* 1992). Differences

in recruitment between this and other locations are not associated with differences in structural complexity of seagrass habitats (McNeill *et al.* 1992). Site B2 is between two man-made structures – a port and an airport runway. These features protrude into the main tidal channel of the bay and lead to the formation of eddies at B2 (SPCC 1979). Planktonic larvae are therefore likely to be directed towards the northern shore, and retained there by eddies. In contrast, there are unlikely to be any such recirculating features on the southern side of the bay adjacent to B1, and any larvae reaching this shore are less likely to be retained there.

The distribution of newly recruited *Pelates* in Pitt Water may also result from estuarine circulation. Currents at the

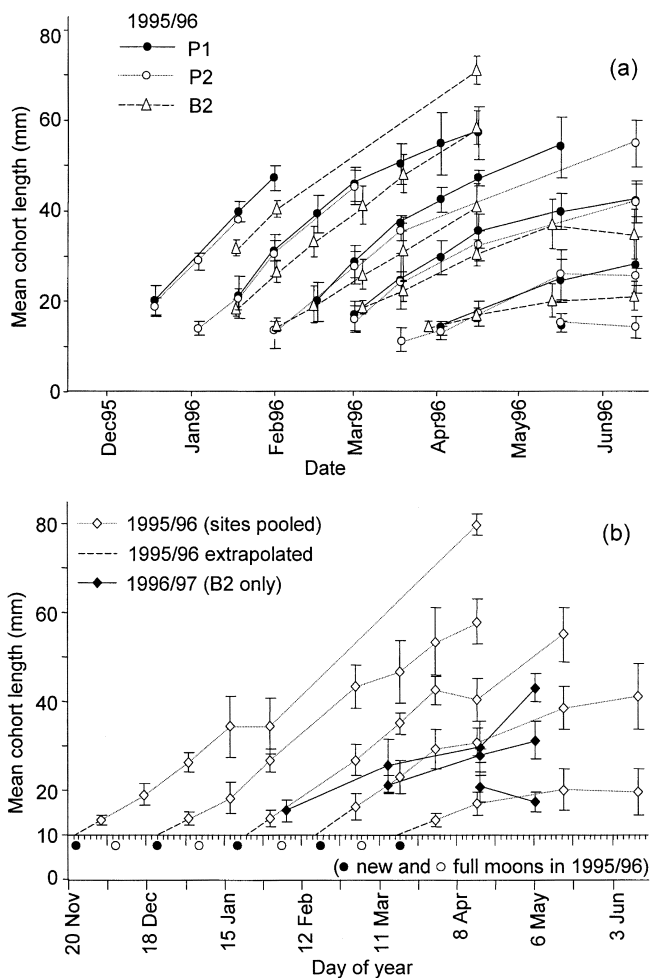


Fig. 8. (a) Mean lengths (\pm s.d.) of *Pelates* cohorts at sites B2, P1 and P2 versus date. (b) Mean lengths (\pm s.d.) of *Pelates* cohorts in 1995/96 (all sites pooled), and cohorts at B2 in 1997, against day of year. Initial sections of growth trajectories for 1995/96 cohorts extrapolated back to 10 mm, to approximate length at settlement.

mouth of Pitt Water during flood tide are directed into the estuary on the western side, but outward on the eastern side (Cox *et al.* 1993; Smith, unpublished). Residual (average) circulation in Pitt Water is negligible in the absence of wind, but thought to circulate in an anti-clockwise direction in the lower part of the estuary during southeasterly winds (Kjerfve *et al.* 1992). This circulation could transport larvae to P2 before P1, despite P1 being closer to the entrance of the estuary. A higher abundance of new recruits and a smaller size at settlement at P2 may have resulted from larval advection to P2 before P1.

In shallow estuaries such as Botany Bay and Pitt Water, wind-driven circulation is likely to influence larval dispersal. A near-surface distribution is also likely to make larvae highly susceptible to wind driven circulation. The limited

observations of *Pelates* larvae have been in surface waters (Miskiewicz 1987; Gray 1995) and settlement stage *Rhabdosargus* larvae swim at the surface within estuarine water (T. Trnski, pers. comm.). Winds may influence broad scale estuarine circulation, as well as small scale or transient features such as estuarine fronts, which may play a role in the advection of larvae (Kingsford and Suthers 1996).

Implications for management of seagrass beds and juvenile fish populations

The results of this, and other studies, suggest that estuarine circulation is partially responsible for spatial patterns of fish recruitment within south-eastern Australian estuaries. The alteration of estuarine flows, such as by dredging or the placement of artificial structures, is likely to alter patterns of fish recruitment. In addition to the restrictions placed on settlement by passive larval advection, are the active processes of habitat selection by recruiting individuals of some species. For example, juveniles of *Rhabdosargus*, recruit primarily to monospecific beds of *Zostera capricorni* on the east Australian coast. Hence, 'successful' recruitment depends not only on advection to a site, but also on the presence of appropriate habitat type. Other species, such as *Pelates*, may be less selective of habitat at settlement (i.e. will settle into other species of seagrass), but become more selective in the weeks to months following settlement. This increases the difficulty of assessing the relative value of different seagrass beds to juvenile fish.

Understanding the recruitment patterns of seagrass fauna will assist in the management of seagrass habitats and fisheries resources. For example, minimizing anthropogenic disturbances within *Zostera capricorni* seagrass from June to November may maximize recruitment success of *Rhabdosargus*. Alternatively, the enhancement of seagrass habitats during recruitment periods, such as through the placement of artificial habitats or opening of coastal lagoons, may increase recruitment rates.

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References

- Bell, J. D., and Westoby, M. (1986). Variation in seagrass height and density over a wide spatial scale: effects on common fish and decapods. *Journal of Experimental Marine Biology and Ecology* **104**, 275–95.
- Bell, J. D., Westoby, M., and Steffe, A. S. (1987). Fish larvae settling in seagrass: do they discriminate between beds of different leaf density? *Journal of Experimental Marine Biology and Ecology* **111**, 133–44.

- Carr, M. H.** (1991). Habitat selection and recruitment of an assemblage of temperate zone reef fishes. *Journal of Experimental Marine Biology and Ecology* **146**, 113–37.
- Cowen, R. K.** (1985). Large scale pattern of recruitment by the labrid, *Semicossyphus pulcher*: Causes and implications. *Journal of Marine Research* **43**, 719–42.
- Cox, D. R., Lee, R. S., and Howden, M. I.** (1993). Sydney deepwater outfalls environmental monitoring program post-commissioning phase. Broken Bay entrance model verification experiment 6 April 1993, Oceanography. Australian Water and Coastal Studies Pty Ltd. Report 93/01/07. (Sydney.) 40 pp.
- Doherty, P., and Fowler, A.** (1994). An empirical test of recruitment limitation in a coral reef fish. *Science* **263**, 935–9.
- Forward, R. B., Tankersley, R. A., and Reinsel, K. A.** (1998). Selective tidal stream transport of spot (*Leiostomus xanthurus* Lacepedé) and pinfish (*Lagodon rhomboides* Linnaeus) larvae: contribution of circatidal rhythms in activity. *Journal of Experimental Marine Biology and Ecology* **226**, 19–32.
- Gray, C. A.** (1995). The influence of sewage plumes and oceanography on assemblages of larval fish. PhD Thesis. University of Sydney.
- Gray, C. A.** (1996). Intrusions of surface sewage plumes into continental shelf waters: interactions with larval and presettlement juvenile fishes. *Marine Ecology Progress Series* **139**, 31–45.
- Hannan, J. C., and Williams, R. J.** (1998). Recruitment of juvenile marine fishes to seagrass habitat in a temperate Australian estuary. *Estuaries* **21**, 29–51.
- Hyndes G. A., Platell, M. E., Potter, I. C., and Lenanton, R. C. J.** (1999). Does the composition of the demersal fish assemblages in temperate coastal waters change with depth and undergo consistent seasonal changes? *Marine Biology* **134**, 335–52.
- Jenkins, G. P., Black, K. P., Wheatley, M. J., and Hatton, D. N.** (1997). Temporal and spatial variability in recruitment of a temperate seagrass-associated fish is largely determined by physical processes in the pre- and post-settlement phases. *Marine Ecology Progress Series* **148**, 23–35.
- Jones, M. B., and Epifanio, C. E.** (1995). Settlement of brachyuran megalopae in Delaware Bay: an analysis of time series data. *Marine Ecology Progress Series* **125**, 67–76.
- Kingsford, M. J.** (1990). Linear oceanographic features: a focus for research on recruitment processes. *Australian Journal of Ecology* **15**, 391–401.
- Kingsford, M. J., and Suthers, I. M.** (1996). The influence of tidal phase on patterns of ichthyoplankton abundance in the vicinity of an estuarine front, Botany Bay, Australia. *Estuarine, Coastal and Shelf Science* **43**, 33–54.
- Kjerfve, B., Seim, H. E., Blumberg, A. F., and Wright, L. D.** (1992). Modelling of the residual circulation in Broken Bay and the Lower Hawkesbury River, NSW. *Australian Journal of Marine and Freshwater Research* **43**, 1339–57.
- Leis, J. M., and Carson-Ewart, B. M.** (1998). Complex behaviour by coral-reef fish larvae in open water and near-reef pelagic environments. *Environmental Biology of Fishes* **53**, 259–66.
- Loneragan, N. R., Potter, I. C., Lenanton, R. C. J., and Caputi, N.** (1986). Spatial and seasonal differences in the fish fauna in the shallows of a large Australian estuary. *Marine Biology* **92**, 575–86.
- McDonald, P. D. M., and Pitcher, T. J.** (1979). Age groups from size–frequency data: a versatile and efficient method of analysing distribution mixtures. *Journal of the Fisheries Research Board of Canada* **36**, 987–1001.
- McNeill, S. E., Worthington, D. G., Ferrell, D. J., and Bell, J. D.** (1992). Consistently outstanding recruitment of five species of fish to a seagrass bed in Botany Bay, NSW. *Australian Journal of Ecology* **17**, 359–65.
- Middleton, J. H., Cox, D., and Tate, P.** (1997). The oceanography of the Sydney region. *Marine Pollution Bulletin* **33**, 124–31.
- Milicich, M. J.** (1994). Dynamic coupling of reef fish replenishment and oceanographic processes. *Marine Ecology Progress Series* **110**, 135–44.
- Miskiewicz, A. G.** (1986). The season and length at entry into a temperate Australian estuary of the larvae of *Acanthopagrus australis*, *Rhabdosargus sarba* and *Chrysophrys auratus* (Teleostei: Sparidae). In ‘Proceedings of the Second International Conference on Indo-Pacific Fishes’. (Eds T. Uyeno, T. Taniuchi and K. Matsuura.) pp. 740–7. (Ichthyological Society of Japan: Tokyo.)
- Miskiewicz, A. G.** (1987). Taxonomy and ecology of fish larvae in Lake Macquarie and New South Wales coastal waters. PhD Thesis. University of New South Wales, Sydney.
- Miskiewicz, A. G. and Neira, F. J.** (1998). Sparidae. In ‘Larvae of Temperate Australian Fishes’. (Eds F. J. Neira, A. G. Miskiewicz, and T. Trnski.) pp. 306–15. (University of Western Australia Press: Perth.)
- Neira, F. J., and Potter, I. C.** (1992). Movement of larval fishes through the entrance channel of a seasonally open estuary in Western Australia. *Estuarine, Coastal and Shelf Science* **35**, 213–24.
- Pollard, D. A.** (1984). A review of ecological studies on seagrass–fish communities, with particular reference to recent studies in Australia. *Aquatic Botany* **18**, 3–42.
- Pollock, B. R., Weng, H., and Morton, R. M.** (1983). The seasonal occurrence of postlarval stages of yellowfin bream, *Acanthopagrus australis* (Günther), and some factors affecting their movement into an estuary. *Journal of Fish Biology* **22**, 409–15.
- Potter, I. C., Loneragan, N. R., Lenanton, R. C. J., Chrystal, P. J., Grant, C. J.** (1983). Abundance, distribution and age structure of fish populations in a Western Australian estuary. *Journal of Zoology* **200**, 21–50.
- Robertson, D. R.** (1992). Patterns of lunar settlement and recruitment in Caribbean reef fishes at Panama. *Marine Biology* **114**, 527–37.
- Robertson, D. R., Green, D. G., and Victor, B. C.** (1988). Temporal coupling of production and recruitment of larvae of a Caribbean reef fish. *Ecology* **69**, 370–81.
- Rothlisberg, P. C., Church, J. A., and Fandry, C. B.** (1995). A mechanism for near-shore concentration and estuarine recruitment of post-larval *Peneus plebejus* Hess (Decapoda, Penaeidae). *Estuarine, Coastal and Shelf Science* **40**, 115–38.
- Roughgarden, J. S., Gaines, S., and Possingham, H.** (1988). Recruitment dynamics in complex life cycles. *Science* **241**, 1460–6.
- Smith, K. A.** (1999). Larval fish distributions and recruitment patterns in the Sydney region with emphasis on the role of physical environmental factors. PhD Thesis. University of New South Wales, Sydney.
- Smith, K. A., Gibbs M. T., Middleton, J. H., and Suthers, I. M.** (1999). Short term variability in larval fish assemblages of the Sydney shelf: tracers of hydrographic variability. *Marine Ecology Progress Series* **178**, 1–15.
- Smith, K. A., and Suthers, I. M.** (1999). Displacement of diverse ichthyoplankton assemblages by a coastal upwelling event on the Sydney shelf. *Marine Ecology Progress Series* **176**, 49–62.
- Sponaugle, S., Cowen, R. K.** (1997). Early life history traits and recruitment patterns of Caribbean wrasses (Labridae). *Ecological Monographs* **67**, 177–202.
- SPCC.** (1979). Tidal water movement in Botany Bay. Environmental Control Study of Botany Bay, Report BBS13. Sydney. 40 pp.
- SPCC.** (1981). The ecology of fish in Botany Bay – Biology of commercially and recreationally valuable species. Environmental Control Study of Botany Bay, Report BBS23. Sydney. 78 pp.
- Thorrold, S. R., Shenker, J. M., Mojica, R., Maddox, E. D., and Wishinski, E.** (1994a). Temporal patterns in the larval supply of summer-recruiting reef fish to Lee Stocking Island, Bahamas. *Marine Ecology Progress Series* **112**, 75–86.

- Thorrold, S. R., Shenker, J. M., Wishinski, E., Mojica, R., and Maddox, E. D.** (1994b). Larval supply of shorefishes to nursery habitats around Lee Stocking Island, Bahamas. I. Small scale distribution patterns. *Marine Biology* **118**, 555–66.
- Tolimieri, N., Sale, P. F., Nemeth, R. S., and Gestring, K. B.** (1998). Replenishment of populations of Caribbean reef fishes: are spatial patterns of recruitment consistent through time? *Journal of Experimental Marine Biology and Ecology* **230**, 55–71.
- Trnski, T. and Neira, F. J.** (1998). Terapontidae. In 'Larvae of Temperate Australian Fishes'. (Eds F. J. Neira, A. G. Miskiewicz and T. Trnski.) pp. 316–23. (University of Western Australia Press: Perth.)
- Wallace, J. H.** (1975) The estuarine fishes of the east coast of South Africa. III. Reproduction. *Investigation Report of the Oceanographic Research Institute* **41**, 1–48.
- Whitfield, A. K.** (1989). Ichthyoplankton interchange in the mouth region of a southern African estuary: *Marine Ecology Progress Series* **54**, 25–33.
- Worthington, D. G., Ferrell, D. J., McNeill, S. E., and Bell, J. D.** (1992). Growth of four species of juvenile fish associated with the seagrass *Zostera capricorni* in Botany Bay, New South Wales. *Australian Journal of Marine and Freshwater Research* **43**, 1189–98.
- Young, P. C.** (1981). Temporal changes in the vagile epibenthic fauna of two seagrass meadows (*Zostera capricorni* and *Posidonia australis*). *Marine Ecology Progress Series* **5**, 91–102.

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