Spatial variation in abundance of recently settled rocky reef fish in southeastern Australia: implications for detecting change

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ABSTRACT: Spatial variation in abundance of recently settled fish was assessed using replicated visual census during 3 surveys of rocky reefs < 12 m deep in New South Wales. Two surveys compared abundances on reefs up to 29 km apart. The third, larger-scale survey compared abundances at 3 levels: regions (100 to 200 km) locations (5 to 12 km) and reefs (1 to 3 km). There were differences in abundance of recently settled individuals among reefs for many species, but these differences were masked by great variability in abundance within reefs. A realistic increase in replication would have greatly increased the chance of detecting significant differences in abundance among reefs for some species. In the larger-scale survey, 9 species settled. Most of the variability in abundance occurred among or within reefs, rather than among locations and regions. The great variability in abundance within reefs at all spatial scales has consequences for assessment of environmental impact on settlement of rocky reef fish. We propose several ways of collecting data that should increase the likelihood of detecting such impact, including selection of control reefs with similar habitats to the impacted reef(s), and counting fish within habitats rather than from transects crossing habitats.

INTRODUCTION

Patchy settlement of juvenile fish among and within habitats has been reported for coral reefs worldwide (Doherty & Williams 1988, Sale 1988), and for temperate reefs in California (Cowan 1985) and New Zealand (Jones 1988). This has been attributed to 2 broad phenomena. First, dispersal of eggs and/or larvae from spawning areas by ocean currents in a largely unpredictable way, with the result that competent larvae are distributed unevenly among suitable habitats. Second, selection of specific conditions at settlement, such as particular habitats or the presence of conspecifics: arrival of larvae at reefs where these conditions are distributed patchily may result in non-uniform settlement. Examples of these phenomena are given by Doherty & Williams (1988), Jones (1988), Sale (1988) and Holbrook et al. (1990).

Most species of fish found on temperate rocky reefs in southeastern Australia have a pelagic larval stage, so we also expect great variation in their settlement within and among reefs. This prediction must be confirmed because data on settlement of juveniles are

necessary for monitoring effects of human impact on rocky reef fish (Underwood 1989, Fairweather 1990). In southeastern Australia, these impacts include ocean disposal of sewage and dredge spoil, construction of breakwaters and strong fishing pressure.

This study was designed to describe spatial variation in settlement of rocky reef fish in part of southeastern Australia, and to assess the suitability of such data for use in sampling designs to detect change. Our methods include testing null hypotheses of no differences in abundance of recently settled fish among reefs, at several spatial scales. We conclude by considering ways of measuring variation in abundance appropriate for assessment of human developments on settlement of rocky reef fish.

METHODS

Study sites and times. Data were collected during 3 surveys of sections of reefs < 12 m deep in New South Wales; one at Port Kembla (34° 29' S, 150° 55' E), another at Sydney (33° 45' S, 151° 15' E), and the third at Sydney (34° 00' S, 151° 11' E), Jervis Bay (35° 03' S,

150° 44' E) and Batemans Bay (35° 44' S, 150 °14' E). The Port Kembla survey compared settlement on 4 reefs on 3 occasions between October 1985 and April 1986. Two of the reefs were ca 3 km apart on nearshore islands; the other 2 were on the mainland and also 3 km apart (Fig. 1). These reefs consist of boulders and shelves with some crustose coralline algae but little algal turf or macroalgae, i.e. the Barrens habitat (sensu Underwood et al. 1991), and intermittent sand patches.

The survey at Sydney compared settlement on 4 reefs twice a year in 1987 and 1988. Three of the reefs were within 7 km of each other, the fourth was 22 to 29 km from the others (Fig. 1). Reefs consisted typically

of the Barrens habitat dominated by large boulders with crevices, intermittent sand patches, and occasional shelves with *Ecklonia* forest habitat (sensu Underwood et al. 1991).

The third survey compared settlement on 2 reefs at each of 2 locations in each of 3 regions up to 200 km apart (Fig. 2). Two censuses were made, one in October 1988, the other in March 1989. Within each region, the 2 locations were 4 to 12 km apart. Within locations, reefs were 1 to 3 km apart. Most reefs consisted of a mosaic of habitats; barrens comprised of boulders, rock shelves dominated by *Ecklonia* forest, turf habitat (sensu Underwood et al. 1991), and sand patches.

Fig. 1 Position of reefs surveyed in Port Kembla and Sydney. The number in brackets beside the name of a reef corresponds to reef number in Tables 1 & 2

Fig. 2. Position of reefs surveyed at 2 locations (north and south) in Sydney, Jervis Bay and Batemans Bay. The number in brackets beside the name of a reef corresponds to reef number in Figs. 3 & 4

Survey procedure. Fishes were counted using the visual techniques of Lincoln Smith (1988, 1989). At each reef, four 60 m transect lines were laid haphazardly. These transects usually spanned the variety of habitats present at the reef. Fish were counted within 1 m of the line using 1 of 2 methods. Conspicuous fishes were recorded while swimming steadily along the entire transect. Cryptic fishes were counted by searching only 30 m of the transect at slow swimming speed (1.7 m min^{-1}). Recently settled fishes (called settlers from here on) were distinguished by their size (< 40 mm total length) and pigmentation. To enable meaningful analysis we decided that a 'settlement event' had occurred for a species when we recorded more than 4 settlers on at least 1 reef on a particular occasion.

Analysis of data. Data from surveys at Port Kembla and Sydney were analysed using 1-way ANOVA when a species settled at 2 or more reefs. When a species settled at only 1 reef, we calculated 95 % confidence limits (CL) for the single mean, and concluded that there was a significant difference among reefs when the lower CL was greater than zero. For some species, settlers were recorded on more than 1 occasion. Since such occasions were several months apart, and the settlers were of the same size, we considered that they represented separate settlement events.

For the survey comparing 3 regions, data for a given species were analysed in 1 of 2 ways. When settlers were recorded on 2 occasions we used a 4-way, mixed model ANOVA to compare the following factors: time (October vs March), region (Sydney vs Jervis Bay vs Batemans Bay), location (sets of reefs > 4 km apart) and (reefs < 3 km apart). Time was orthogonal to region, location and reef, while reef was nested in location and region, and location was nested within region. When settlers were recorded on only 1 occasion, the analysis was reduced to a fully nested design comparing region, location and reef. Post hoc pooling of non-

significant factors (p ≥ 0.25) followed Winer (1971). After analysis, the percentage of variation explained by each factor was calculated (Winer 1971).

Prior to analysis, data were tested for heteroscedasticity using Cochran's Test, and transformed as necessary. Where data remained heteroscedastic after transformation, alpha was set below the probability of the Cochran's value (0.025 or 0.01 as appropriate) to reduce the Type I error rate (Underwood 1981). When significant differences among means were found using ANOVA, Student Newman Keuls (SNK) tests were used to isolate them. The same alpha was used for the ANOVA and SNK tests.

For all surveys, we also used the coefficient of variation, CV (standard deviation/mean) as a measure of within-reef variability. Where CV ≥ 1.0, we considered within-reef variability to be high.

For settlement events at Port Kembla and Sydney, we assessed the power of the analysis (Cohen 1988) to detect arbitrarily chosen differences in abundances of settlers among reefs.

RESULTS

Surveys at Port Kembla and Sydney

A total of 20 settlement events were recorded in these surveys. They fell into 4 groups (Tables 1 & 2). First, species with significant differences in abundance among reefs, but low variability (CV < 1.0) in abundance within reefs (2 events). Second, species with significant differences in abundance among reefs, and high variability (CV ≥ 1.0) within reefs (2 events). Third, species showing no significant difference in abundance among reefs but high variability within reefs (15 events). Fourth, species showing no significant difference in abundance among reefs and low variability within reefs (1 event).

Survey of 3 regions

Species that settled twice

Abundances of the 3 species that settled at both times did not vary significantly among locations (Table 3). There were, however, other significant sources of variation in their settlement. For abundance of *Trachinops taeniatus* there was a significant interaction between time and region (Table 3, Fig. 3a). In October, more individuals settled in Sydney than in other regions, but in March there was no difference among regions (SNK tests, n = 16). Significant variation in settlement also occurred among reefs (Table 3). In Sydney, more fish settled at Reefs 2 and 3 than at Reef 4, but there were no significant differences among reefs in the other 2 regions (SNK tests, n = 8). Within-reef variability was high (Fig. 3a) and accounted for > 60 % of the variance (Table 3).

Table 1. Mean abundance (x̄) and coefficient of variation (CV) for untransformed abundances of recently settled fish (arranged under families in taxonomic order) at 4 reefs (1 to 4) in Port Kembla (Fig. 1). Note that there were 2 settlement events for 3 of the species. Also shown are results for 1-way ANOVA comparing abundances on reefs, or analysis of 95 % confidence limits (CL) associated with mean abundance, on data transformed to ln (x + 1); ns: p > 0.05, • p ≤ 0.05

Species	Date	x̄ (CV)				ANOVA (df: 3,12)	CL
		1	2	3	4		
Scorpaenidae							
Scorpaena cardinalis	Jan 1986	0	0	0	2.8 (0.3)	–	ns
S. cardinalis	Apr 1986	0.5 (2.0)	0.8 (2.0)	2.5 (1.0)	1.8 (0.3)	ns	–
Dinolestidae							
Dinolestes lewini	Jan 1986	0	0	4.5 (1.4)	0.3 (2.0)	ns	–
Mullidae							
Parupeneus signatus	Jan 1986	0	0	3.5 (2.0)	5.0 (2.0)	ns	–
P. signatus	Apr 1986	0	0	2.0 (1.2)	4.5 (1.2)	ns	–
Pempherididae							
Pempheris multiradiata	Jan 1986	0	0	8.8 (1.4)	7.3 (1.4)	ns	–
Scorpididae							
Atypichthys strigatus	Oct 1985	0	0	8.0 (1.4)	0	–	ns
A. strigatus	Jan 1986	0	0	14.8 (0.3)	0	–	•
Scorpis lineolatus	Oct 1985	0	0	6.0 (2.0)	0	–	ns
Pomacentridae							
Parma microlepis	Jan 1986	4.0 (0.7)	3.5 (2.0)	6.0 (0.4)	7.0 (1.2)	ns	–
Cirrhitidae							
Cirrhitichthys aprinus	Apr 1986	0	0	2.5 (1.1)	0	–	ns

Table 2. Mean abundance ($\bar{x}$) and coefficient of variation (CV) for untransformed abundances of recently settled fish (arranged under families in taxonomic order) at 4 reefs in Sydney (Fig. 1). Note that there were 2 settlement events for 2 of the species. Also shown are results for 1-way ANOVA comparing abundances on reefs, or analysis of 95% confidence limits (CL) associated with mean abundance, on data transformed to ln $(x + 1)$; ns: $p > 0.05$, * $p \leq 0.05$, ** $p \leq 0.01$

Species	Date	$\bar{x}$ (CV)				ANOVA (df: 3,12)	CL
		1	2	3	4		
Serranidae							
Ellerkeldia mccullochi	Jan 1988	1.3 (0.8)	0.3 (2.0)	0	0	*	–
E. mccullochi	Apr 1987	14.8 (0.3)	0	0	0	–	**
Plesiopidae							
Trachinops taeniatus	Jan 1988	75.5 (1.0)	8.0 (1.8)	11.5 (1.5)	0	**	–
Pempherididae							
Pempheris compressus	Apr 1987	0	0	0	8.5 (1.3)	–	ns
Pempheris multiradiata	Jan 1988	0	2.0 (0.9)	0	10.5 (2.0)	ns	–
Scorpididae							
Atypichthys strigatus	Jan 1988	5.5 (1.8)	13.5 (1.2)	11.8 (1.1)	0.3 (2.0)	ns	–
Pomacentridae							
Chromis hypsilepis	Apr 1987	0	0.3 (2.0)	1.3 (2.0)	1.8 (1.2)	ns	–
C. hypsilepis	Jan 1988	0.3 (2.0)	1.0 (2.0)	0.8 (1.3)	1.3 (1.5)	ns	–
Parma microlepis	Jan 1988	5.3 (0.5)	12.3 (0.5)	7.8 (1.3)	5.3 (0.5)	ns	–

Abundance of *Pempheris multiradiata* differed significantly among reefs (Fig. 3b). In Jervis Bay, more individuals settled at Reef 5 than at any other reef, and in Batemans Bay, more settled at Reef 10 than at Reef 11 (SNK tests, n = 8). Variation within reefs explained 61% of the variance in abundance of *P. multiradiata* (Table 3).

There was no significant difference in abundance of *Parma microlepis* among reefs within regions in October, but there were significant differences in March (SNK tests, n = 4). Then, more settlers were seen at Reef 1 than at any other reef in Sydney; fewer occurred at Reef 7 than at any other reef in Jervis Bay; and there were more at Reefs 9 and 12 than at Reef 10 in Batemans Bay. Sampling time explained most of the variation in abundance of *P. microlepis* (Table 3), although considerable variation was apparent within some reefs in October (Fig. 3c).

Species that settled once

One species settled only during October and 5 settled only during March (Table 3). In October, *Atypichthys strigatus* varied significantly in abundance between locations, but only in Jervis Bay (Table 3; SNK tests, n = 8), where recruitment occurred over a scale of about 5 km (see Fig. 2 for distances between locations). Location accounted for 52% of the variance, and variation within reefs was relatively high (Table 3, Fig. 4a).

Abundance of *Ellerkeldia mccullochi* varied significantly among reefs, but only in Sydney (Table 3). There were greater abundances at Reef 1 than at all other reefs, and Reefs 2 and 3 had more settlers than Reef 4. Within-reef variability was low (Table 3, Fig. 4b), and most of the variance was found at greater spatial scales (Table 3).

For *Parupeneus signatus*, *Schuettea scalaripinnis*, *Pempheris compressus*, and *Chromis hypsilepis*, there was no significant difference in abundance among regions, locations or reefs (Table 3). Instead, variability within reefs was very high for each species (Table 3, Fig. 4c to f). Region, location and reef made no contribution to variance in abundance of *Schuettea scalaripinnis*.

Power analyses

In the surveys at Port Kembla and Sydney there were large ($\geq$ 2-fold), but non-significant differences in abundance among reefs for 14 of 20 settlement events (Tables 1 & 2). We assessed the power of our survey design to detect 5-fold and 10-fold differences in abundance of settlers among reefs when the species occurred at all reefs in each area, and where the greatest differences among means were $\leq$ 5-fold. Four settlement events met these criteria (Table 4). We created the 5-fold and 10-fold differences by increasing the values of the data for the reef that had the greatest mean. We also calculated the number of replicate transects needed to achieve power of 0.80 (i.e. a 20% chance of making a Type II error) when looking for such differences.

Our surveys had low power ($\leq$ 0.40) to detect a 10-fold difference in abundance among reefs for 2 of the settlement events, but power was high ($\geq$ 0.75) for

Table 3. Summary of ANOVAs of abundances of recently settled reef fish among regions, location and reefs in October 1988 and March 1989. Where a species settled in both months, time is included as a factor in the model. The variance explained by each component of the model is also shown. l: data transformed to ln(x + 1); r: data transformed to √(x + 1), +: Cochrans test non-significant at alpha = 0.025, ++: alpha = 0.01; ns: p > 0.05, $^{\cdot}$ $p \leqslant 0.05$, $^{\cdot\cdot\cdot}$ $p \leqslant 0.001$

Type of species	Settlement period	Factors in ANOVA							
		Time	Region	Loc.	Reef	T × Reg.	T × L	T × Reef	Res.
Species that settled twice									
Plesiopidae									
Trachinops taeniatus l	Oct/Mar	ns	ns	ns	•	•••	ns	ns	
Variance (%)		0	0	0	10.8	25.1	0	2.6	61.5
Pempherididae									
Pempheris multiradiata l++	Oct/Mar	ns	ns	ns	•••	ns	ns	ns	
Variance (%)		0.10	0	11.1	26.4	0.1	1.3	0	61.0
Pomacentridae									
Parma microlepis r	Oct/Mar	•••	ns	ns	•••	ns	ns	•	
Variance (%)		63.7	0	3.2	4.8	5.6	0	7.6	15.2
Species that settled once									
Serranidae									
Ellerkeldia mccullochi l++	March	−	ns	ns	•••	−	−	−	
Variance (%)			37.2	12.7	28.7				21.3
Mullidae									
Parupeneus signatus l+	March	−	ns	ns	ns	−	−	−	
Variance (%)			0	15.7	0				84.3
Monodactylidae									
Schuettea scalaripinnis l	March	−	ns	ns	ns	−	−	−	100
Variance (%)			0	0	0				
Pempherididae									
Pempheris compressus l++	March	−	ns	ns	ns	−	−	−	
Variance (%)			0	0.7	15.9				83.4
Scorpididae									
Atypichthys strigatus	October	−	ns	•	ns	−	−	−	
Variance (%)			0	57.9	0				42.1
Pomacentridae									
Chromis hypsilepis l	March	−	ns	ns	ns	−	−	−	
Variance (%)			11.0	6.7	15.9				66.3

detecting such differences for the other 2 events (Table 4). Power was low for detecting a 5-fold difference among reefs for 3 of the 4 events (Table 4). Between 3 and 9 replicates were needed to detect a 10-fold difference in means with power of 0.80, whereas 5 to 14 replicates were required to achieve comparable power when looking for a 5-fold difference.

DISCUSSION

Surveys at Port Kembla and Sydney demonstrated that abundance of settlers was often highly variable within reefs. For the majority of settlement events in these surveys such variability swamped substantial differences among reefs. In some cases, e.g. settlement of *Parma microlepis* in Sydney during January 1988, small increases in replication would have permitted detection of a 5-fold difference among reefs with a Type II error rate of 20 %. In other cases, e.g. settlement of *Chromis hypsilepis* at Sydney in January 1988, variability was so great that it was logistically impossible to achieve the replication needed to have an analysis with comparable power.

Another feature of our results was that, for some species, variation in abundance of settlers among reefs differed among times within the large-scale survey, or between surveys at Port Kembla and Sydney. This has consequences for the design of future sampling. For example, one would conclude from the Sydney data that *Parma microlepis* could be used to detect 5-fold differences among reefs if replication was increased to
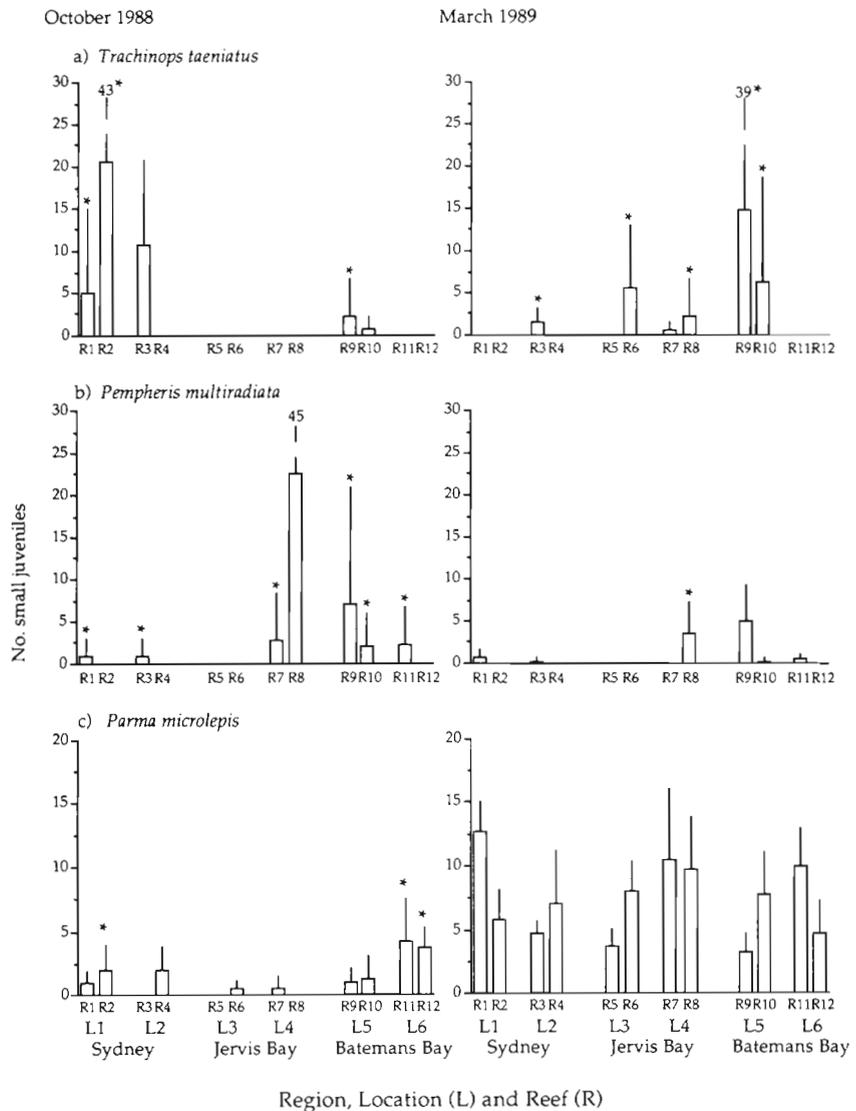
Fig. 3. Mean (n = 4) abundance of (a) *Trachinops taeniatus* (b) *Pempheris multiradiata*, and (c) *Parma microlepis* at 2 reefs (R) in each of 2 locations (L) in 3 regions during October 1988 and March 1989. Vertical bars are 1 standard deviation. *CV for the mean exceeded 1.0. See Fig. 2 for names of reefs at each location

5 transects or more. However, at Port Kembla, this species would have been appropriate for detecting such differences only if 9 transects were done.

High variability in abundance of recently settled fish within reefs, and apparent high variability among reefs, is not surprising. The reefs we studied had many features believed to promote and maintain spatial variability in settlement of fish. The reefs were isolated from one another by bare substrata, thus larvae settling in large numbers on one reef were unlikely to migrate to another (see Bell & Westoby 1986 for arguments why there should be selection against recently settled fish leaving shelter and crossing bare substrata). The reefs also had a variety of habitats. This would help maintain within-reef variability by enabling individuals to select habitats that enhance survival (Bell & Westoby 1986, Jones 1988, Holbrook et al. 1990). We have made

several observations consistent with this view. Abundances of *Parma microlepis* and *Ellerkeldia mccullochi* appear to be correlated positively with topographic complexity, *Pempheris compressus* and *Pempheris multiradiata* occur only in narrow crevices, and *Atypichthys strigatus* are most common on small sand patches within and beside reefs.

Other factors that may account for variability within and among reefs are post-settlement processes, such as mortality, and the observer's ability to detect juveniles at a given size after settlement (Keough & Downes 1982). So, variability may depend on the time at which the species was counted relative to the original settlement event, and the size at which the species could be detected and identified. Further work, possibly involving intensive surveys over narrow time scales to follow the fate of settlers, is needed on these subjects.
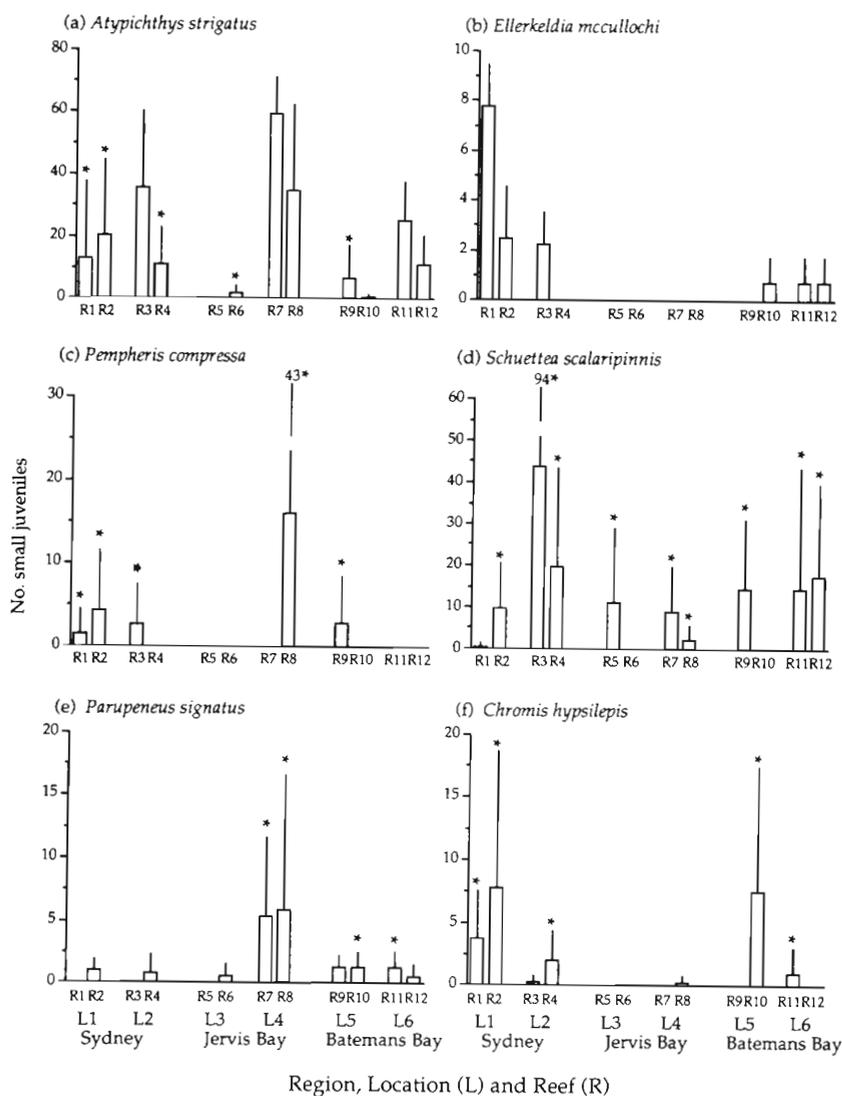
Fig. 4. Mean (n = 4) abundance of (a) *Atypichthys strigatus*, (b) *Ellerkeldia mccullochi* (c) *Pempheris compressus*, (d) *Schuettea scalaripinnis*, (e) *Parupeneus signatus* and (f) *Chromis hypsilepis* at 2 reefs (R) in each of 2 locations (L) in 3 regions. Vertical bars are 1 standard deviation. *CV for the mean exceeded 1.0. See Fig. 2 for names of reefs at each location

The large variability in abundances of recently settled fishes on rocky reefs has implications for assessing the impact of human activities. We do not propose to discuss the design of surveys to detect impact as this subject has been covered by others, e.g. Green (1979), Stewart-Oaten et al. (1986), Underwood (1989). However, our data indicate that natural variation in abundance of recently settled rocky reef fish within reefs can be great enough to make detection of changes among reefs very difficult. In situations where it is important to document change in abundance of settlers caused by development it will be essential to maximize the power of the analysis and reduce variability in the data. Our studies suggest 3 ways of doing this.

First, increase the frequency of sampling, the number of reefs sampled and/or the number of replicates per reef. Recall that the survey of 3 regions

often found significant differences in abundance among reefs despite great variability within reefs. Also, power analysis showed that small increases in replication for surveys at Port Kembla and Sydney greatly increased the chance of detecting statistically significant differences among reefs for some species. (See Underwood 1989 for a discussion of the effects of frequency and spatial scale of sampling on detection of perturbations in populations.)

Second, consider selecting control reefs on the basis of physical similarity rather than simply on the basis of proximity. If most variation in settlement of a species is at the 'within-reef' scale, then it is important that control reefs should have similar topography, habitats, exposure to currents, etc. as the impacted reef(s).

Third, count fish in discrete habitats, rather than from transects spanning several habitats. This last measure

Table 4. Power of the sampling design used in this study to detect 5-fold and 10-fold differences between means in abundance of recently settled individuals for selected settlement events at Port Kembla (PK) and Sydney (S). The number of replicates needed to detect such differences when power is 0.80 are also shown; ND indicates that the number of replicates could not be determined

Species	Time	Area	5-fold		10-fold	
			Power	n	Power	n
Scorpaena cardinalis	Apr 1986	PK	0.23	14	0.40	9
Chromis hypsilepis	Jan 1988	S	0.0	ND	0.0	ND
Parma microlepis	Jan 1986	PK	0.39	9	0.75	5
Parma microlepis	Jan 1988	S	0.71	5	1.00	3

depends on knowing the habitat requirements of a species, and the other biological processes, including interactions with other species, that affect their settlement. This information remains to be gathered for most species of fish associated with rocky reefs in southeastern Australia.

In conclusion, this paper evaluated the implications of settlement patterns of rocky reef fish, rather than merely describing them. In particular, the use of power analysis allowed us to evaluate non-significant results and to quantify our alternative hypotheses. The selection of 5- and 10-fold differences as alternative hypotheses was arbitrary because we did not have sufficient information to select more specific alternatives. An important component of future studies will be the gathering of data on natural variability in abundance of settling fish. Without this, alternative hypotheses for testing the effects of human impact on settlement events cannot be refined.

LITERATURE CITED

Bell, J. D., Westoby, M. (1986). Variation in seagrass height and density over a wide spatial scale: effects on common fish and decapods. J. exp. mar. Biol. Ecol. 104: 275–295

Cohen, J. (1988). Statistical power analysis for the behavioral sciences, 2nd edn. Lawrence Erlbaum Associates, New Jersey

Cowan, R. K. (1985). Large scale pattern of recruitment by the labrid, *Semicossyphus pulcher*: causes and implications. J. mar. Res. 43: 719–742

Doherty, P. J., Williams, D. McB. (1988). The replenishment of coral reef fish populations. Oceanogr. mar. Biol. A. Rev. 26: 487–551

Fairweather, P. (1990). Implications of 'supply-side' ecology for environmental management. Trends Ecol. Evol. 16: 60–63

Green, R. H. (1979). Sampling design and statistical methods for environmental biologists. John Wiley and Sons, New York

Holbrook, S. J., Schmitt, R. J., Ambrose, R. F. (1990). Biogenic habitat structure and characteristics of temperate reef fish assemblages. Aust. J. Ecol. 15: 489–504

Jones, G. P. (1988). Ecology of rocky reef fish of north-eastern New Zealand: a review. N.Z. J. mar. Freshwat. Res. 22: 445–462

Keough, M. J., Downes, B. J. (1982). Recruitment of marine invertebrates: the role of active larval choices and early mortality. Oecologica 54: 348–352

Lincoln Smith, M. P. (1988). Effect of observer swimming speed on sample counts of temperate rocky reef fish assemblages. Mar. Ecol. Prog. Ser. 43: 223–231

Lincoln Smith, M. P. (1989). Improving multispecies rocky reef fish censuses by counting different groups of species using different procedures. Environ. Biol. Fish. 26: 29–37

Sale, P. F. (1988). Perception, pattern, chance and the structure of reef fish communities. Environ. Biol. Fish. 21. 3–15

Stewart-Oaten, A., Murdoch, W. W., Parker, K. R. (1986). Environmental impact assessment: 'pseudoreplication' in time? Ecology 67: 929–940

Underwood, A. J. (1981). Techniques of analysis of variance in experimental marine biology and ecology. Oceanogr. mar Biol. A. Rev. 19: 513–605

Underwood, A. J. (1989). The analysis of stress in natural populations. Biol. J. Linn. Soc. 37: 51–78

Underwood, A. J., Kingsford, M. J., Andrew, N. L. (1991). Patterns in shallow subtidal marine assemblages along the coast of New South Wales. Aust. J. Ecol. 16: 231–250

Winer, B. J. (1971). Statistical principles in experimental design, 2nd edn. McGraw-Hill, New York