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Shane Griffiths
University of Wollongong

Ronald West
University of Wollongong, ron@uow.edu.au

Andrew R. Davis
University of Wollongong, adavis@uow.edu.au

Ken Russell
University of Wollongong, kerussell@csu.edu.au

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Griffiths, Shane; West, Ronald; Davis, Andrew R.; and Russell, Ken, "Fish recolonization in temperate Australian rockpools: a quantitative experimental approach" (2004). *Faculty of Science, Medicine and Health - Papers: part A*. 1905.
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Fish recolonization in temperate Australian rockpools: a quantitative experimental approach

Abstract

Understanding recolonization processes of intertidal fish assemblages is integral for predicting the consequences of significant natural or anthropogenic impacts on the intertidal zone. Recolonization of experimentally defaunated intertidal rockpools by fishes at Bass Point, New South Wales (NSW), Australia, was assessed quantitatively by using one long-term and two short-term studies. Rockpools of similar size and position at four sites within the intertidal zone were repeatedly defaunated of their fish fauna after one week, one month, and three months during two short-term studies in spring and autumn (5 months each), and every six months for the long-term study (12 months). Fish assemblages were highly resilient to experimental perturbations— recolonizing to initial fish assemblage structure within 1–3 months. This recolonization was primarily due to subadults (30–40 mm TL) and adults (>40 mm TL) moving in from adjacent rockpools and presumably to abundant species competing for access to vacant habitat. The main recolonizers were those species found in highest numbers in initial samples, such as *Bathygobius cocosensis, Enneapterygius rufopileus*, and *Girella elevata*. Defaunation did not affect the size composition of fishes, except during autumn and winter when juveniles (<30 mm>TL) recruited to rockpools. It appears that Bass Point rockpool fish assemblages are largely controlled by postrecruitment density-dependent mechanisms that indicate that recolonization may be driven by deterministic mechanisms.

Keywords

experimental, quantitative, approach, rockpools, fish, australian, temperate, recolonization

Disciplines

Medicine and Health Sciences | Social and Behavioral Sciences

Publication Details

Griffiths, S. P., West, R. J., Davis, A. R. & Russell, K. G. (2004). Fish recolonization in temperate Australian rockpools: a quantitative experimental approach. Fishery Bulletin, 102 (4), 634-647.

This journal article is available at Research Online: https://ro.uow.edu.au/smhpapers/1905

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Manuscript submitted 28 April 2003 to the Scientific Editor's Office.

Manuscript approved for publication 5 May 2004 by the Scientific Editor.

Fish. Bull. 102:634–647 (2004).

Fish recolonization in temperate Australian rockpools: a quantitative experimental approach

Shane P. Griffiths

Environmental Science

and

Institute for Conservation Biology
University of Wollongong
Wollongong, New South Wales, Australia
Present address: CSIRO Marine Research
233 Middle Street
Cleveland, Queensland 4163 Australia

Email address: shane.griffiths@csiro.au

Ron J. West

Environmental Science
University of Wollongong
Wollongong, New South Wales, Australia

Andy R. Davis

Institute for Conservation Biology
University of Wollongong
Wollongong, New South Wales, Australia

Ken G. Russell

School of Mathematics and Applied Statistics
University of Wollongong
Wollongong, New South Wales, Australia

Rocky intertidal fishes are faced with many biotic (competition and food availability) and abiotic (temperature and salinity) factors that can influence their distribution and abundance (Gibson, 1982). Despite occupying a dynamic environment, the fish assemblages in intertidal rockpools have been widely shown to remain persistent through time (Grossman, 1982, 1986; Collette, 1986). These communities can also rapidly return to their original state after major or even catastrophic perturbations (Moring, 1996). Such resilience is less common among assemblages of invertebrates (Connell, 1972; Astles, 1993) because recolonization of substrata is normally dependent upon successful larval settlement (Paine and Levin, 1981). In contrast, fish can rapidly colonize available habitat by larval recruitment from the plankton (Willis and Roberts, 1996, Beckley, 2000; Griffiths 2003a) but also by the relocation of subadults and adults from adjacent rockpools (Beckley, 1985a; Griffiths, 2003a). Under natural conditions rockpools can be defaunated by events such as hurricanes (Moring, 1996) and, in some regions, by seasonal freezing of rockpool water (Thomson and Lehner, 1976; Moring, 1990). These events can create new microhabitats or open existing ones for fish to colonize, and therefore have the potential to change fish assemblage structure.

Understanding recolonization processes of intertidal fish assemblages is integral for predicting the consequences of natural or anthropogenic impacts on the intertidal community. The role of disturbance and recolonization processes in structuring inter-

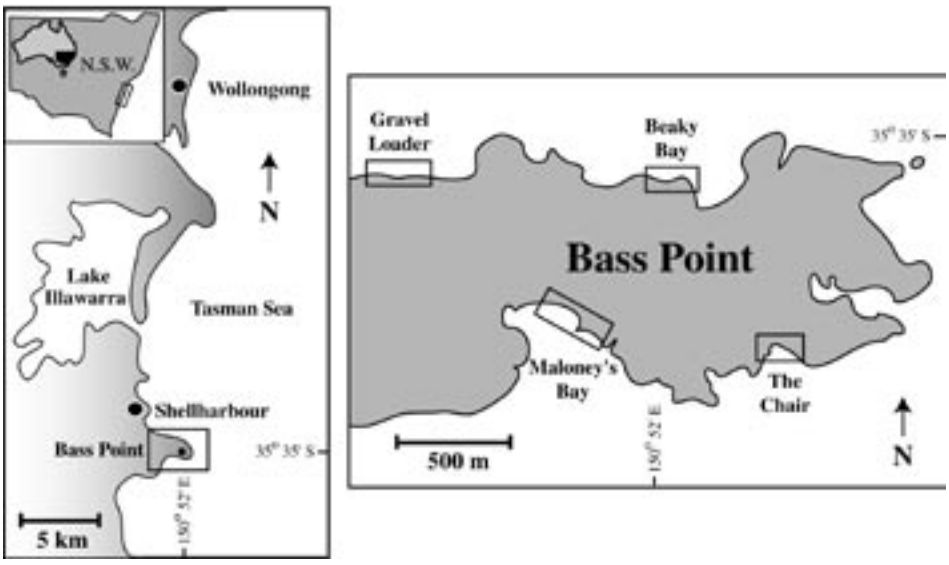


Figure 1

Map illustrating the four sampling sites at Bass Point and the location of the study location in the Illawarra region, New South Wales, Australia.

tidal rockpool fish assemblages has received considerable attention in many countries of the world (Bussing, 1972; Matson et al., 1986; Yoshiyama et al., 1986; Prochazka and Griffiths, 1992; Lardner et al., 1993; Prochazka, 1996; Faria and Almada, 1999; Silberschneider and Booth, 2001). Such studies have identified patterns in the rates of recovery, variation in species and size composition of recolonizing fish assemblages (Polivka and Chotkowski, 1998; Beckley, 2000), and homing abilities of many intertidal fishes (Green 1971; Yoshiyama et al., 1992; Griffiths, 2003b).

Rockpools can be regarded as "island' habitats (Underwood and Skilleter, 1996) among an inhospitable rocky landscape. Therefore, there is probably a balance between immigration (recruitment and relocation) and emigration (mortality) of fishes after a disturbance, *sensu* the equilibrium theory of island biogeography (MacArthur and Wilson, 1967). After a period of time, the number of species and individuals in a defaunated rockpool can be expected to reach an asymptote when a carrying capacity is reached. It is difficult to generalize about recolonization rates of rockpools by fishes from the current literature mainly owing to the diversity of methods used, their differing effectiveness in sampling fish, and the varying intensity of the sampling regime. For example, most studies have used only small sample sizes (<10 pools) and have sampled at a range of time intervals from days (Mistry et al., 1989; Matson et al., 1986; Polivka and Chotkowski, 1998) to years (Thomson and Lehner, 1976; Lardner et al., 1993; Mahon and Mahon, 1994). A second problem in measuring and comparing fish recolonization patterns between studies is that many researchers have sampled fish using an anesthetic (Mahon and Mahon, 1994; Pfister, 1995, 1997) or ichthyocide (Beckley, 1985a, 1985b, 2000; Willis and Roberts, 1996; Silberschneider and Booth, 2001), which may affect subsequent catches (Yoshiyama et al., 1986) and possibly result in fish assemblages never reaching preperturbation conditions (see Mok and Wen, 1985; Lockett, 1998).

Nonetheless, recolonization of rockpools by fishes is generally a rapid process, beginning within days, or even hours, after defaunation (Collette, 1986), and complete recolonization to preperturbation levels can take a few weeks (Collette, 1986; Faria and Almada, 1999) to several months (Mok and Wen, 1985; Willis and Roberts, 1996; Polivka and Chotkowski, 1998).

The aims of this study were to quantitatively determine 1) the period required for intertidal rockpools to recover to preperturbation levels, 2) the fish species (permanent residents, opportunist, or transients) responsible for recolonizing rockpools, 3) whether recolonization patterns differ between the four sites at Bass Point and between the times of year when defaunation took place, and 4) whether fish comprise different life-history stages before and after a disturbance (sampling)—by examination of length-frequency distributions.

Methods

Study site and experimental design

Spatial and temporal variation in fish recolonization patterns were investigated in three separate studies undertaken along the north- and south-facing rocky platforms at Bass Point (34°58′S, 150°93′E), New South Wales, Australia (Fig. 1). Bass Point is a large rocky headland that extends approximately 3 km into the Tasman Sea. Two short-term recolonization studies (each around 5

months in duration) were undertaken in spring–summer and autumn–winter (hereafter referred to as spring and autumn studies, respectively), and a long-term recolonization study spanned a 12-month period. Rockpools for each of the three studies were selected at four sites at Bass Point, NSW, which are named Maloney's Bay (MB), The Chair (TC), Gravel Loader (GL), and Beaky Bay (BB) (Fig. 1). Each of the four sites are separated by about 1 km. Rockpools were selected at each site (50–200 m apart) according to similar physical parameters (i.e., volume, surface area, and substrate type) and particularly according to their vertical elevation on the rock platform. Because higher pools might have less chance of fish recolonization because they are less frequently inundated by seawater (Griffiths et al., 2003), every effort was made to select pools located in the mid-intertidal zone (1–1.5 m above MLLW [mean lower low water]) and, although pools were visually similar, they varied in volume, ranging from 762 to 2160 liters (or 0.76–2.16 m^3). The bottom of the rockpools consisted of pebbles, cobbles, and small boulders.

For the short-term studies, four rockpools were sampled and fish removed at each of the four sites. In the spring study (beginning 7 September 1999), they were then resampled 1 week, 1 month, and 3 months after the preceding sampling date (referred to as the "1-week," "1-month," and "3-month" samples in this article). This study ended on 8 February 2000, after a period of 5 months. After this date a period of at least three months was given for pools to re-establish fish assemblages before beginning the autumn study on 15 May 2000. Rockpools were sampled in exactly the same manner as for the spring study, with sampling ending on 17 September 2000. For each study, 64 samples were taken giving a total of 128 samples for the short-term studies. It is important to note that although every effort was made to resample pools after exactly the same time intervals, this was not possible because of daily time and height of tides and wave heights. For example, for the "1 week" samples, the number of days between samples was actually between 7 and 10 days.

To determine whether frequent sampling in the short-term studies affected the structure of rockpool fish assemblages, a long-term study was undertaken by using four different rockpools at the same four sites that were sampled in the short-term studies. Four rockpools at each site were considered adequate because Griffiths (2003a) was able to detect significant differences in the numbers of fish species and individuals in rockpools between sites and months using four rockpools per site in the same region that was surveyed in our study. Rockpools were initially sampled on 22 September 1999 and then resampled twice at intervals of six months (20 April 2000 and 11 September 2000). A total of 48 samples were taken for this study.

Data collection

Fish were collected by hand after completely emptying each rockpool with a VMC 12V battery-powered bilge pump of 9029 L/h capacity by using the methods of Griffiths (2000). A thorough search of each pool was conducted by overturning all rocks and boulders, searching all crevices and shaking algal fronds until all fish that could be seen were removed. Fishes were identified and total lengths (TL) were measured. Fork length (FL) was also measured for economically significant species. Fish were categorized as being juveniles (<30 mm), subadults (30–40 mm), or adults (>40 mm). Fish were then released alive into rockpools or the shallow subtidal 10–30 m away from the rockpool being sampled, which was considered to be the approximate distance that fish may be displaced by waves and surge during significant natural disturbances, such as storms. Each species was categorized by its residential status in rockpool habitats according to the definitions of Griffiths (2003c) in order to better understand the types of fish responsible for recolonization. These categories were "permanent residents," "opportunists," and "transients."

Statistical analyses

A repeated-measures ANOVA (RM-ANOVA) was used (SPSS vers. 6.1; SPSS, Chicago, IL) to test for significant differences in the numbers of species and individuals between sampling intervals (within-subjects factor) and sites (among-subjects factor). Short- and long-term experiments were analyzed with two separate RM-ANOVAs. For the short-term study a third factor of season (i.e., spring or autumn; among-subjects factor) was added. All factors were considered fixed. Assumption of sphericity of the variance-covariance matrix was tested by using Mauchly's criterion and, if violated, F tests were performed with Greenhouse-Geisser–adjusted degrees of freedom. Student-Newman-Keuls (SNK) tests were used for *a posteriori* comparisons among means (numbers of species and individuals) in RM-ANOVAs.

Nonmetric multidimensional scaling (nMDS) was used to examine similarities in fish assemblage structure between sampling intervals and sites. Data were fourth-root transformed, to reduce the influence of highly abundant taxa, and a similarity matrix was constructed by using the Bray-Curtis similarity coefficient (Clarke, 1993). Stress values are given for all ordination plots; these values describe the quality of the representation of multidimensional relationships of the data in a two-dimensional plane. Stress factors of less than 0.2 (<0.2 is considered to give a good representation of sample "relatedness" and to prevent the prospect of drawing false inferences) were obtained for each ordination (Clarke, 1993).

Analysis of similarities (ANOSIM) was used to test whether fish assemblages in *a priori* groups differed statistically (Clarke, 1993). Abundance data for each species were pooled for the four rockpools at each site and time. Each ANOSIM comparison involved generating 4999 random permutations of the data to calculate the probability that observed differences in the structure of the fish assemblages among *a priori* groups could arise

by chance. Similarity percentages (SIMPER) were used to determine which species were responsible for differences between selected groups. This analysis involved calculating the average contribution of each species in each pair of groups and comparing this contribution to the overall dissimilarity of fish assemblages between the groups. All multivariate analyses were carried out with PRIMER (Plymouth routines in multivariate ecological research) software (version 5.2.2, PRIMER-E Ltd., Roborough, Plymouth, UK).

Results

Composition of rockpool fish assemblages

A total of 3658 fish representing 38 species and 19 families was caught in 176 samples from 32 rockpools at Bass Point between 7 September 1999 and 22 September 2000 (Table 1), corresponding to densities of 0.5 and 19 species/m^3 (mean 4.4 [±2.9] /m^3) and 0.5 and 80 fish/m^3 (mean 15.6 [±14.6] /m^3), respectively. The most numerically abundant taxa were permanent rockpool residents representing the families Gobiidae (*Bathygobius cocosensis*), Tripterygiidae (*Enneapterygius rufopileus*), Clinidae (*Heteroclinus whiteleggi* and *H. fasciatus*), Blenniidae (*Parablennius intermedius*), and Gobiesocidae (*Aspasmogaster costatus*), although the temporary resident *Girella elevata* was the third most abundant species. The ten most numerically abundant species represented 92% of the catch (Table 1). Three species, *G. elevata*, *Scorpis lineolatus,* and *Myxus elongatus*, represented by 504 fish were considered to be of economic significance. All economically important fishes were caught as juveniles in the rockpools and 89% of the fish measured less than 100 mm FL.

Numbers of species and individuals

For the short-term studies, the mean number of species differed significantly between sampling intervals and sites (RM-ANOVA, Table 2). With respect to the site factor, there were significantly more species caught at BB than at the other three sites and the latter three sites did not differ from each other (SNK test). Only the "1-week" samples accounted for significantly fewer species than the initial samples (Fig. 2). However, the mean number of species caught in the "1-month" and "3-month" samples did not differ significantly from the initial samples at all sites (Fig. 2).

The mean number of individuals differed significantly between sampling intervals and sites, although there was also a significant *time*×*site* interaction (RM-ANOVA, Table 2). A close investigation of the significant *interval*×*site* interaction, with primary interest in the interval factor, revealed that the number of individuals in the initial samples did not differ significantly from samples taken after three months at the exposed sites (MB and TC), but they did differ significantly at sheltered locations (GL and BB) (Fig. 2). It appeared that the

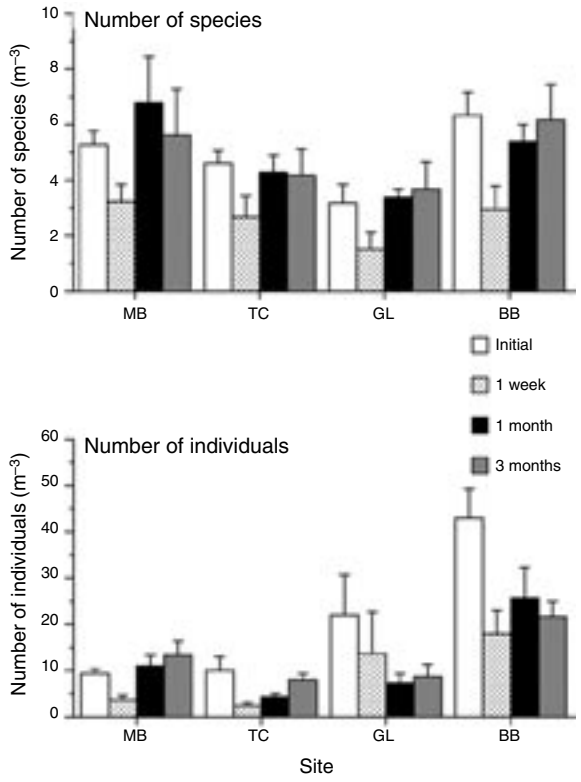


Figure 2

Mean (±SE) numbers of species and individuals (m^{-3}) caught in rockpools at Bass Point, New South Wales between 7 September 1999 and 17 September 2000 during the short-term recolonization studies (combined for spring and autumn) between sampling intervals separated by 1 week, 1 month, and 3 months. Key to sites: Maloney's Bay (MB), The Chair (TC), Gravel Loader (GL), Beaky Bay (BB).

Loader and Beaky Bay sites initially supported unusually high numbers of individuals and these high numbers may have accounted for significantly fewer individuals caught in the subsequent samples (Fig. 2).

For the long-term study, the number of individuals significantly differed among sampling times but did not for number of species (RM-ANOVA, Table 3). The significant difference in the mean number of individuals was due to fewer individuals caught in the "12-month" samples when fish numbers were pooled for all sites (SNK test, Fig. 3).

Variation in abundance of major recolonizing species

The rank abundances of the numerically dominant species were consistent for *B. cocosensis* and *E. rufopileus* across all sampling intervals for all studies, even though their relative abundances varied considerably (Table 4). In contrast, the ranks of the least common of the six species, namely *H. whiteleggi*, *P. intermedius*,

Table 1

Numbers of fish for each species caught from rockpools at four sites at Bass Point, NSW, during short-term (spring and autumn) and long-term recolonization studies conducted between 7 September 1999 and 22 September 2000. * = species of commercial or recreational significance (or both).

Family and scientific name	Spring study	Autumn study	Long-term study	Total
Muraenidae				
Gymnothorax prasinus	41	13	16	70
Gymnothorax cribroris	1	—	—	1
Plotosidae				
Cnidoglanis macrocephalus	1	—	—	1
Gobiesocidae				
Alabes dorsalis	—	2		2
Aspasmogaster costatus	134	41	65	240
Aspasmogaster liorhyncha	5	20	4	29
Syngnathidae				
Urocampus carinirostris	1	—	—	1
Scorpaenidae				
Scorpaena cardinalis	1	—	—	1
Serranidae				
Acanthistius ocellatus	33	35	16	84
Epinephelus daemelii	—	2	—	2
Plesiopidae				
Trachinops taeniatus	1	—	—	1
Girellidae				
*Girella elevata**	210	93	74	377
Scorpididae				
Microcanthus strigatus	1	—	—	1
*Scorpis lineolatus**	94	10	16	120
Pomacentridae				
Abudefduf vaigiensis	1	—	—	1
Parma microlepis	—	1	—	1
Chironemidae				
Chironemus marmoratus	30	11	10	51
Mugilidae				
*Myxus elongatus**	3	4	—	7
Labridae				
Halichoeres nebulosus	—	1	—	1
Notolabrus gymnogenis	—	1	—	1
Blennidae				
Parablennius intermedius	102	78	47	227
Istiblennius meleagris	8	10	4	22
Tripterygiidae				
Lepidoblennius haplodactylus	22	26	22	70
Norfolkia clarkei	7	4	3	14
Enneapterygius rufopileus	354	188	157	699
Clinidae				
Heteroclinus fasciatus	59	48	38	145
Heteroclinus nasutus	1	—	—	1
Heteroclinus heptaeolus	24	—	1	25
Heteroclinus johnstoni	—	2	—	2
Heteroclinus whiteleggi	138	66	39	243
Ophiclinus gracilis	15	16	6	37

continued

Table 1 (continued)

Family and scientific name	Spring study	Autumn study	Long-term study	Total
Gobiidae				
Bathygobius cocosensis	583	293	285	1161
Callogobius depressus	6	2	7	15
Callogobius mucosus	1	—	—	1
Priolepis cincta	1	—	—	1
Gobiidae sp.	1	—	—	1
Microdesmidae				
Gunnellichthys monostigma	1	—	—	1
Tetraodontidae				
Torquigener pleurogramma	—	1	—	1
Totals	1880	968	810	3658

Table 2

Results of repeated-measures ANOVAs for significant differences in numbers of species and number of individuals (/m^3) caught at Bass Point during two short-term recolonization studies among sampling intervals (time) (within-subjects factor), seasons (spring and autumn) and sites (among-subjects factors). Both numbers of species and individuals data were $\log_{10}(x+1)$ transformed before analysis, which removed heteroscedasticity in the data. Mauchly's criterion for sphericity of variances was violated for number of species (P=0.025); therefore the analysis was performed with Greenhouse-Geisser–adjusted degrees of freedom. Mean squares (MS) and significance levels are shown and significant results are given in boldface. * = P<0.05; ** = P<0.01; *** = P<0.001.

	Number of species		Number of fish	
Source	df	MS	df	MS
Among subjects				
Season (*Se*)	1	14.94	1	1292.24
Site (*S*)	3	**46.80****	3	**2782.52****
S×*Se*	3	3.66	3	63.53
Residual	24	9.38	24	370.27
Within subjects				
Time (*T*)	2.16	**18.03*****	3	**825.70*****
T×*S*	6.47	2.93	9	**247.99****
T×*Se*	2.16	2.54	3	94.86
T×*S*×*Se*	6.47	1.89	9	137.84
Residual	51.75	1.41	72	79.71
Mauchly's criterion *W*		**0.569***		0.625

Table 3

Results of repeated-measures ANOVAs for significant differences in numbers of species and number of individuals (/m^3) caught at Bass Point during the long-term recolonization study among sampling intervals (within-subjects factor) and sites (among-subjects factors). Both numbers of species and individuals data were $\log_{10}(x+1)$ transformed before analysis, which removed heteroscedasticity in the data. Mean squares (MS) and significance levels are shown and significant results are given in bold. ** = P<0.01.

	Number of species		Number of individuals
Source	df	MS	MS
Among subjects			
Site (*S*)	3	86.93	176.18
Residual	12	27.49	169.67
Within subjects			
Time (*T*)	2	3.26	**451.38****
T×*S*	6	4.44	111.82
Residual	24	2.84	55.45
Mauchly's criterion *W*		0.622	0.705

and *A. costatus*, varied considerably among sampling intervals for each study. This result probably reflects their generally low abundances, because differences in ranks can be a result of a few incidences of low individual counts.

The mean number of the six most abundant recolonizing species showed considerable variability in space and time. For the short-term study, densities of these species differed significantly among sites and among time intervals or at least for higher order interactions containing these effects (Table 5). No definitive conclusions could be made regarding the effects of defaunation on these species because short-term recolonization patterns for each species were clearly variable within and among seasons (Fig. 4). However, the mean number of fish was generally highest in initial samples and low-

Table 4

Ranked abundances of the six most abundant species overall for each sampling interval in the spring, autumn, and long-term experiments. Total numbers of fish caught during each sampling occasion from 16 rockpools from four sites are shown in parentheses. 1=initial samples; 2=samples taken after 1 week; 3=samples taken after 1 month; 4=samples taken after 3 months. Species having equally ranked abundances are denoted by an "=" sign.

	Spring study				Autumn study				Long-term study		
Species	1	2	3	4	1	2	3	4	1	2	3
Bathygobius cocosensis	1 (153)	1 (69)	1 (73)	1 (59)	2 (81)	1 (20)	1 (58)	1 (41)	1 (115)	1 (114)	1 (63)
Enneapterygius rufopileus	2 (109)	2 (50)	4 (33)	2 (46)	1 (84)	2 (12)	2 (29)	3 (25)	2 (73)	2 (43)	2 (41)
Girella elevata	3 (46)	3 (36)	3 (40)	3 (38)	3 (34)	3 (10)	3 (16)	5 (13)	5 (5)	6 (3)	4 (12)
Heteroclinus whiteleggi	6 (11)	=4 (7)	2 (51)	5 (35)	6 (9)	=4 (5)	6 (7)	2 (37)	6 (4)	4 (27)	6 (8)
Parablennius intermedius	4 (27)	=4 (7)	6 (10)	6 (23)	=4 (14)	=4 (5)	4 (15)	4 (23)	4 (14)	5 (14)	3 (19)
Aspasmogaster costatus	5 (21)	=4 (7)	5 (13)	4 (36)	=4 (14)	6 (3)	5 (8)	6 (7)	3 (22)	3 (34)	5 (9)

est in the 1-week samples at each site for the majority of dominant species. For the long-term study only the mean number of *B. cocosensis* and *E. rufopileus* differed significantly among sampling times (Table 5), and this difference was due to lower numbers being caught in the 12-month samples (Fig. 4).

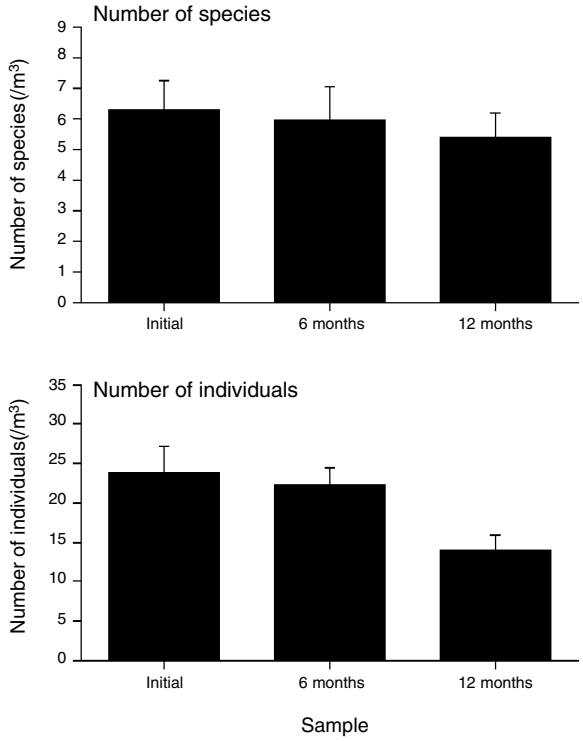


Figure 3

Mean (±SE) numbers of species and individuals (/m^3) caught in rockpools at Bass Point, New South Wales, between 22 September 1999 and 11 September 2000 (pooled for all four sites) during the long-term recolonization study. Intervals between sampling for the long-term study were six months.

Fish assemblage structure

No clear patterns emerged in the nMDS ordination plots, with the exception of separation of the "1 week" samples from all other samples at BB during the autumn study (Fig. 5). ANOSIM supported these visual interpretations of ordination plots and revealed that fish assemblages did not differ significantly among sampling times at any of the four sites for the spring and long-term studies (Table 6) because abundant species *E. rufopileus*, *B. cocosensis*, *H. fasciatus,* and *P. intermedius* were common in all samples (SIMPER analysis). For the autumn study, the results of ANOSIM complemented those of RM-ANOVA in that significant differences among sampling intervals were detected only at BB (Table 6). At this site the initial samples and "1-week" samples differed significantly in their fish assemblages, which was due to higher numbers of *G. elevata* and *B. cocosensis* in the initial samples (SIMPER analysis).

Length-frequency distributions

Removal of fishes from rockpools did not have any apparent effects on the length-frequency distributions for at least two species (*B. cocosensis* and *E. rufopileus*) for which there were sufficient data to construct length-frequency histograms. Unfortunately, the less abundant recolonizing species, namely *P. intermedius*, *A. costatus,* and *H. whiteleggi*, were caught in too few numbers to ascertain the impacts of defaunation on their size compositions. Rockpools were mainly recolonized by subadults and adults for *B. cocosensis* and *E. rufopileus* in all three studies (Figs. 6 and 7). However, cohorts of small juveniles (15–30 mm) were evident in the "3-month" samples during spring and the initial autumn studies (February to June), which could then be clearly identified in subsequent samples (Figs. 6 and 7).

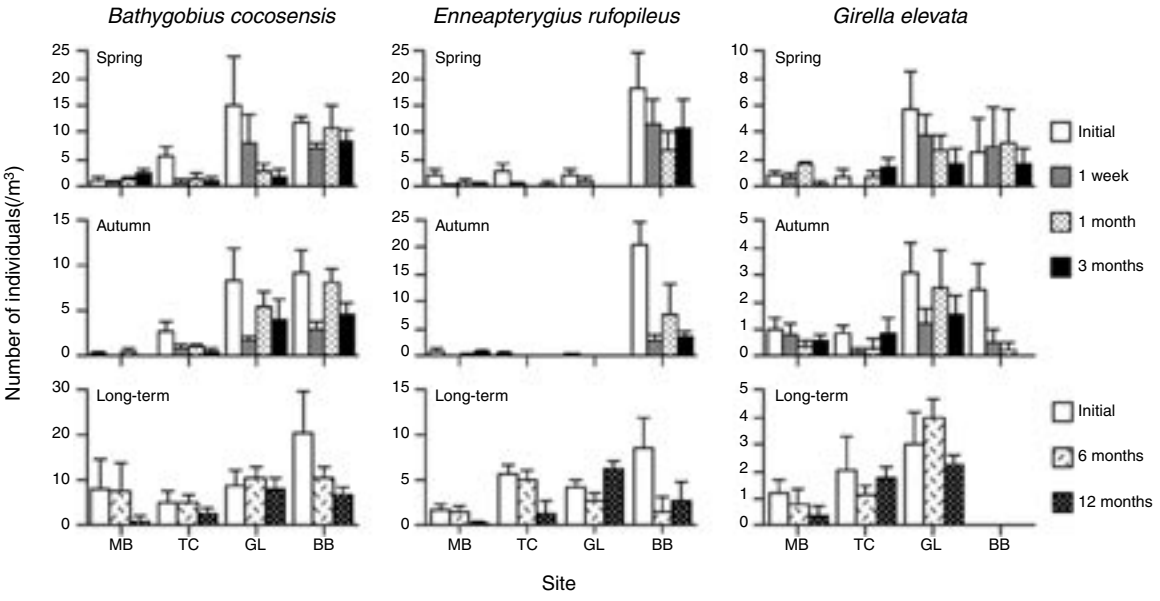


Figure 4

Mean (±SE) numbers of fish (/m^3) for the six most abundant species caught from rockpools at four sites (MB=Maloney's Bay, TC=The Chair, GL=Gravel Loader, BB=Beaky Bay) during short-term (spring and autumn) (four sampling events) and long-term (three sampling events) recolonization studies undertaken between 7 September 1999 and 22 September 2000.

Table 5

Results of repeated-measures ANOVAs for significant differences in numbers of individuals (/m^3) representing the six most abundant species caught at Bass Point during the short-term recolonization studies among sampling intervals (within-subjects factor) and sites and seasons (among-subjects factors). Data were $\log_{10}(x+1)$ transformed before analysis to remove heteroscedasticity in the data. Mauchly's criterion for sphericity of variances was violated ($P<0.001$) for species denoted by ^{G}; therefore analysis was performed using Greenhouse-Geisser–adjusted degrees of freedom. Greenhouse-Geisser degrees of freedom used for within-subjects factors where Mauchly's criterion for sphericity of variances was violated ($P<0.001$): *Time* (T) = 1.55; $Se\times T$ = 1.55; $S\times T$ = 4.64; $Se\times S\times T$ = 4.64; Residual = 34.14. Mean squares and significance levels are shown and significant results are given in bold. Degrees of freedom are shown in parentheses. * = $P<0.05$; ** = $P<0.01$; *** = $P<0.001$.

	Among-subjects factors				Within-subjects factors				
Species	Season (*Se*) (1)	Site (*S*) (3)	*Se*×*S* (3)	Residual (24)	Time (*T*) (3)	*Se*×*T* (3)	*S*×*T* (9)	*Se*×*S*×*T* (9)	Residual (72)
Bathygobius cocosensis^G	5.20	**24.50*****	3.62	2.18	**43.99*****	2.21	**10.68****	3.22	1.70
Enneapterygius rufopileus^G	0.66	**4.38*****	0.01	0.17	**0.70*****	0.05	**0.08***	**0.07***	0.04
Girella elevata	0.22	0.49	0.03	0.28	**0.12****	0.07	**0.05***	**0.07****	0.03
Heteroclinus whiteleggi^G	12.09	**20.77***	1.65	4.90	**18.99*****	**6.61***	**4.31***	4.22	1.72
Parablennius intermedius	0.00	**4.85***	0.20	1.20	**7.88****	0.20	1.92	0.29	1.07
Aspasmogaster costatus	0.37	**0.54****	0.15	0.10	**0.11***	0.09	0.03	**0.07***	0.03

Discussion

This study has shown that fish assemblages can quickly return to preperturbation levels after significant disturbance. This resilience appears to be driven mainly by postsettlement movements of fishes, although recruitment may periodically play a significant role in population replenishment. Not only does this provide an insight into the ecology of rockpool fish assemblages, but this information may also provide a basis for future sampling protocols where the confounding effects of sampling may be minimized.

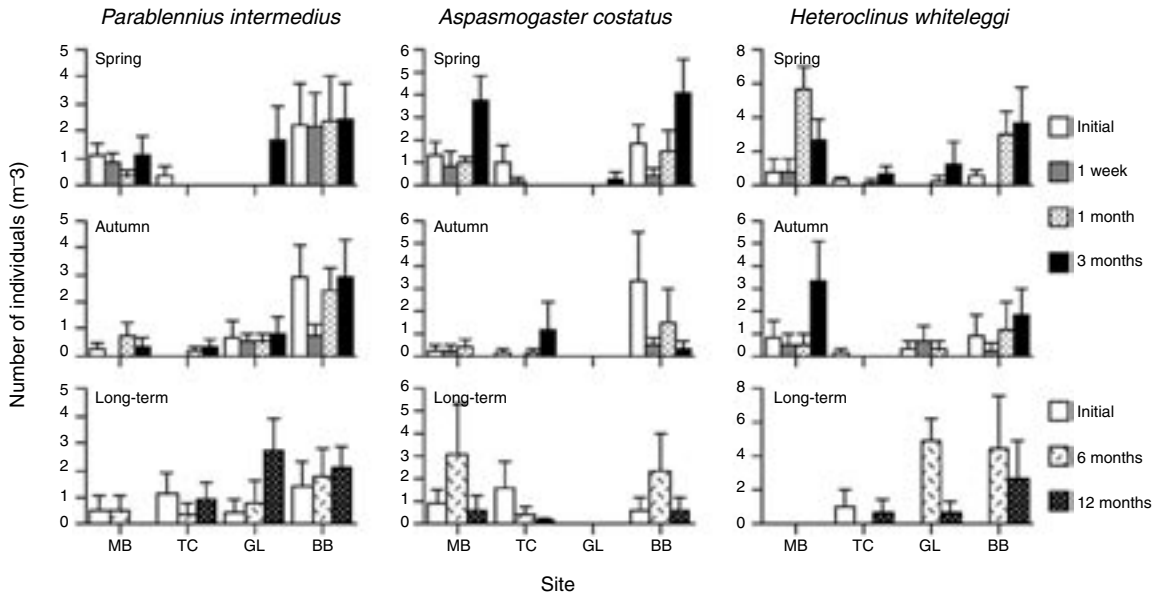


Figure 4 (continued)

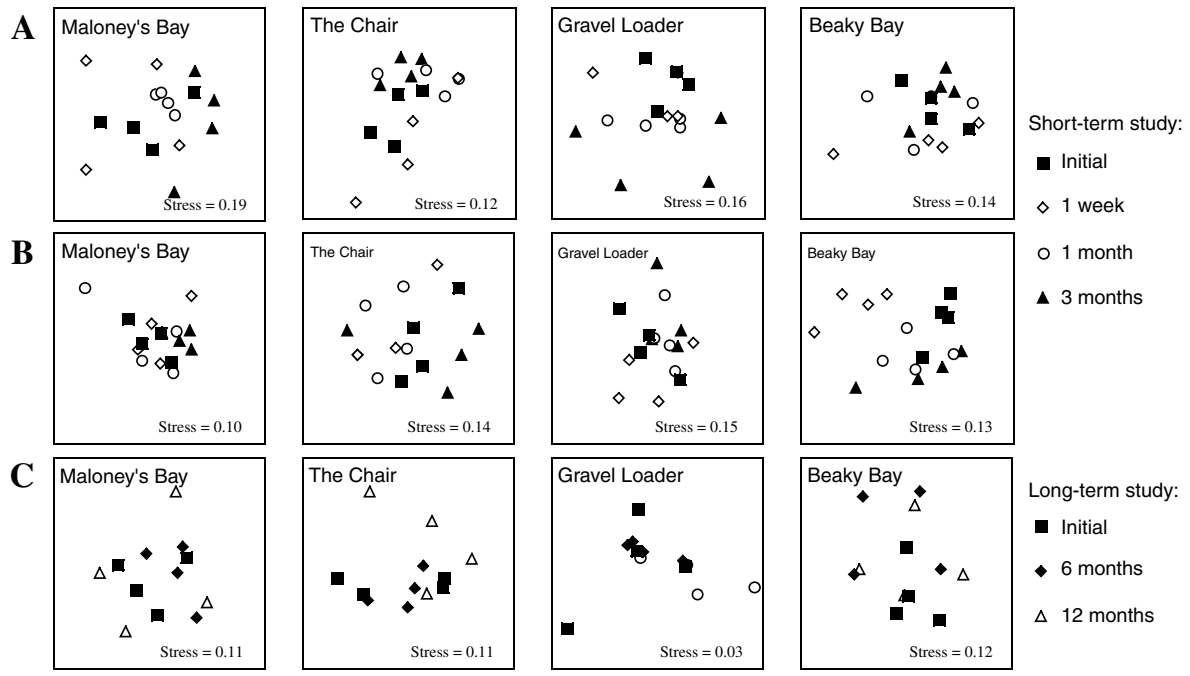


Figure 5

Nonmetric multidimensional scaling (MDS) plots for comparison of fish assemblages from four sites at Bass Point in respect to initial samples and those taken after 1 week, 1 month, and 3 months during (**A**) spring and (**B**) autumn short-term studies, and after 6 months and 12 months during (**C**) the long-term study. Each coordinate represents a single rockpool sample. Stress values are shown.

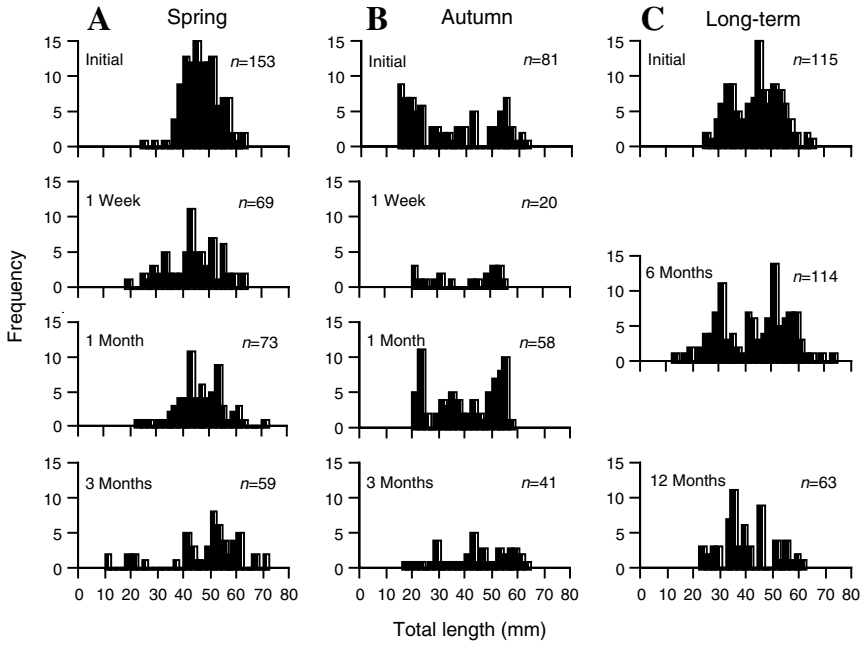


Figure 6

Length-frequency distributions (in 2-mm intervals) for *Bathygobius cocosensis* caught in the initial samples and after 1 week, 1 month, and 3 months later in the short-term study and caught in the initial sampling and 6 months and 12 months later in the long-term study. Samples were pooled for all sites during the (**A**) spring and (**B**) autumn short-term recolonization studies and for all sites during (**C**) the long-term recolonization study. Studies were conducted between 7 September 1999 and 22 September 2000. Samples sizes are shown.

Table 6

Results of ANOSIM testing for differences in fish assemblage structure among sampling intervals at four sites at Bass Point during the spring, autumn, and long-term recolonization studies. Significant results are shown in bold.

	Spring		Autumn		Long-term	
Site	*R*	*P* value	*R*	*P* value	*R*	*P* value
Maloney's Bay	0.002	0.474	0.029	0.393	–0.101	0.752
The Chair	0.185	0.057	0.014	0.422	0.063	0.284
Gravel Loader	0.083	0.165	0.027	0.389	0.190	0.051
Beaky Bay	0.025	0.383	0.726	**0.000**	0.044	0.348

For rockpool fish assemblages in southeastern Australia, a period of one week appears insufficient for recolonization of all species if fish are removed during sampling, whereas intervals of one to three months appear sufficient for rockpool fish assemblages at most Bass Point locations to recolonize to preperturbation levels. It is possible that recolonization times may be decreased if all fish are returned to rockpools immediately after sampling. However, this should not provide a foundation for subsequent studies with other defaunation methods, such as anesthetics or ichthyocides. The possible residual effects of these other sampling methods, such as the mortality of mobile and sessile invertebrates or the residues from chemical anesthetics and ichthyocides are possible factors that may complicate fish recolonization patterns (see Lockett, 1998) and certainly require additional investigation. Nonetheless, in recolonization studies with chemical sampling methods similar recolonization times as those of the present study were found. For example, recolonization of rockpools defaunated by ichthyocides was shown to be complete within 1 month (Grossman, 1982; Prochazka, 1996) and 3 months (Beckley, 1985a; Willis and Roberts, 1996; Polivka and Chotkowski, 1998).

Spatial variability in fish recolonization patterns was not definitive with regard to species composition

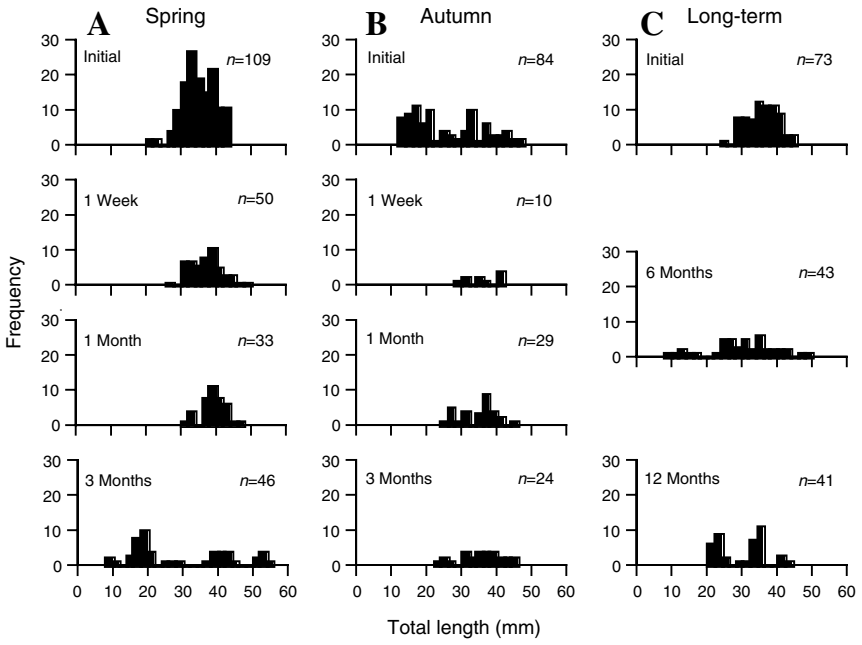


Figure 7

Length-frequency distributions (in 2-mm intervals) for *Enneapterygius rufopileus* caught in the initial samples and after 1 week, 1 month, and 3 months later in the short-term study and caught in the initial sampling and 6 months and 12 months later in the long-term study. Samples were pooled for all sites during the (**A**) spring and (**B**) autumn short-term recolonization studies and for all sites during (**C**) the long-term recolonization study. Studies were conducted between 7 September 1999 and 22 September 2000. Samples sizes are shown.

because samples were generally widely dispersed in nMDS ordination plots. The relatively low stress values (<0.2) indicate that high variability in fish assemblages at the level of individual rockpools is probably responsible for the patterns observed. However, some spatial variability in fish recolonization patterns was evident (Fig. 2) and appeared to be dependent to some extent on exposure of sites to predominant swell. There is evidence to suggest that wave exposure can affect the distribution of intertidal fishes (Gibson, 1972; Ibanez et al., 1989), although there is apparently no study that has investigated this effect in relation to fish recolonization in rockpools. In the present study, recolonization appeared more rapid at wave-exposed sites (MB and TC) compared to more sheltered sites. This may have been the result of the close distance between rockpools at exposed sites (within meters of each other), whereas at both sheltered sites, rockpools were significantly farther apart. Consequently, defaunated rockpools at exposed sites may recolonize more quickly if the major recolonizers are derived from neighboring rockpools as has been documented elsewhere (Beckley, 1985a; Polivka and Chotkowski, 1998).

Fish recolonization patterns were not influenced by the time of year that rockpools were defaunated in either short-term or long-term studies. The numbers of species and individuals consistently returned to pre-perturbation levels within a few weeks, but this return to previous levels may partially be a consequence of the relatively small number of species that are normally found in rockpools at any given time. In such situations a significant differences could only occur if large-scale changes in abundances were recorded. The lack of temporal variation in recolonization rates was surprising because recolonization was expected to be more rapid during summer, when the larvae of residents and warm water transients are expected to be available for settlement (Beckley, 1985a; Willis and Roberts, 1996). Recruitment was not the major mechanism driving fish recolonization in the present study because the majority of recolonizers were subadults and adults that would have relocated from nearby rockpools. Although many of the fish captured in each pool were tagged, the vast majority of fish caught in the same rockpool in subsequent sampling events were not tagged. Griffiths (2003b) showed that the common recolonizing species in the present study moved between a few rockpools within a limited home range. Therefore, postsettlement fishes from surrounding rockpools were probably moving into the study rockpools between each sampling event.

The movement of postsettlement fishes from adjacent rockpools also appears to control the resilience of rock-

pool fish assemblages. Therefore, the composition of species in newly recolonized rockpools is probably dependent upon the relative abundances of species in nearby rockpools. Species having the highest local abundances, such as *B. cocosensis* and *E. rufopileus*, are therefore more likely to be the primary recolonizers because vacant habitats have a higher probability of being located by these species during high-tide excursions throughout the intertidal zone (also see Polivka and Chotkowski, 1998). These species are also versatile and can exploit a range of microhabitats and, as a result, can occupy almost any rockpool within the intertidal zone (Griffiths et al., 2003). This is particularly true for *B. cocosensis*. In contrast, less abundant species such as *H. whiteleggi* often occupy more specific, and perhaps less abundant, microhabitats such as algal cover (see Marsh et al., 1978; Bennett and Griffiths, 1984) that may require longer periods to locate than more abundant habitats, such as cobble-covered substratum.

Processes regulating fish assemblages

The structure of multispecies assemblages can be regarded as being regulated by either deterministic or stochastic processes (see Grossman, 1982). Assemblages regulated by deterministic processes generally occur in environments where conditions are constant or fluctuate consistently over time. The structure of these assemblages is generally predictable. This can be maintained through a number of factors including partitioning of resources in finite supply (Schoener, 1974; Behrents, 1987) and interspecific competition, which prevents any single species being competitively dominant (Buss and Jackson, 1979).

In contrast, assemblages regulated by stochastic processes generally exist in unpredictable environments. Here, the resources are available on a random or periodic basis, which prevents superior competitors from dominating the assemblage (Sale, 1977, 1978). The success of particular species can be compared to winning a "lottery" for living space (Sale, 1977, 1978, 1982). Consequently, stochastically regulated assemblages are generally species rich (Sale, 1977).

Rockpool fish assemblages are often persistent for lengthy periods, even after catastrophic natural disturbances, such as hurricanes (Moring, 1996), and continual experimental eliminations (Grossman, 1982; Collette, 1986). For example, Collette (1986) found two species—*Pholis gunnellus* and *Tautogolabrus adspersus*—to be dominant over 19 years of study in two New England rockpools, whereas the rank of dominant species in the rockpools of Barbados showed no evidence of change over six years (Mahon and Mahon, 1994). Similar stability and persistence were evident in the present study, where *B. cocosensis*, *E. rufopileus* and *G. elevata* were consistently the highest ranked species in each collection for all three studies, regardless of the period between sampling. This finding may indicate that deterministic processes probably regulate the Bass Point fish assemblage. If this is the case, it may seem ironic because the intertidal zone is subjected to a high frequency of stochastic events. It would be easy to assume that such events could eliminate fishes from rockpools and thus leave microhabitats for other species to exploit. This kind of process has been documented for some sessile intertidal invertebrate assemblages that rely on the availability of vacant substrata for successful recruitment of larvae (see examples by Raffaelli and Hawkins, 1996). However, the locomotory capabilities and morphological and physiological adaptations of resident intertidal fishes allow them to cope with such disturbances by being able to cope temporarily with adverse conditions (Martin, 1995). As a result, the abundance of resident species may be little affected under normal disturbance regimes.

Conclusions

The results of this study have significantly increased an understanding of the patterns of recolonization of rockpools by fishes and some of the processes that underpin these patterns. Such an understanding of recolonization processes may improve our ability to predict the consequences of significant natural and anthropogenic disturbances on not only the fish assemblages but also on other intertidal community assemblages that may be maintained by the presence of fish (see Coull and Wells, 1983; Connell and Anderson, 1999).

On a more technical note, the recolonization rates observed in the present study may provide insight for other researchers aiming to study natural temporal variation of rockpool fish assemblages by minimizing the possibility of confounding effects of sampling. This may be particularly important for long-term monitoring programs, such as for marine protected areas (MPAs), that may require detection of changes in community structure over time. Finding sufficient numbers of similar-size pools at a single location for monitoring can be difficult; therefore repeated visits to the same rockpools may often be required. For southeastern Australian rockpools, we feel that a period of one to three months is required before resampling the same rockpools with the methods employed in this study. Although fish were not returned to rockpools immediately after sampling in the present study, we feel that this practice may significantly increase recolonization rates. However, the results of the present study should not provide a foundation for studies using other defaunation methods, such as anesthetics or ichthyocides, because other factors, such as chemical residues remaining in rockpools, may complicate fish recolonization patterns. Further investigation into these other factors will be necessary in the future.

Acknowledgments

We sincerely thank Jade Butler and Alan Griffiths for help with fieldwork. This paper is partly based upon

research included in a Ph.D. by S. P. Griffiths funded by an Australian Postgraduate Award. Additional funding was granted by the Institute for Conservation Biology, University of Wollongong, Shellharbour City Council, The Ecology Lab. Pty. Ltd., and Ocean Beach Hotel Fishing Club. S. P. Griffiths would like to thank CSIRO Marine Research for support during the preparation of this article.

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