Recolonization of Experimentally Defaunated Tidepools by Northeast Pacific Intertidal Fishes

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Site fidelity and maintenance of home ranges are common in fishes (e.g., Stephens et al., 1970; Robertson and Sheldon, 1979; Hixon, 1981), especially for intertidal species for which the ability to navigate to a safe region of an environment that periodically drains of water may be adaptive (e.g., Gibson 1967, 1969, 1982). For intertidal fishes in the northeast Pacific region, homing capabilities have been described in the cottids *Clinocottus analis* (Richkus, 1978), *C. globiceps* (Green, 1973), *Oligocottus maculosus* (Green, 1971; Khoo, 1974; Craik, 1981), and *Oligocottus snyderi* (Williams, 1957; Halverson, 1982; Yoshiyama et al., 1992). The adaptive value of homing in intertidal fishes has not been fully explained, but it is of sufficient ecological benefit to have arisen independently in fishes of different lineages (e.g., Cottidae, Blenniidae) and in different geographical. regions (western North American coast, Britain; Yoshiyama et al., 1992; Gibson, 1967). Aside from its possible benefits in the search for food and escape from desiccation or predators, the ability to home may be used by fishes requiring refuge from hydrodynamic stresses imposed by waves (Chotkowski, 1994).

Despite the apparent importance of site fidelity and homing ability in intertidal fishes, even species that show such localization behaviors have substantial segments of their populations that are vagile and presumably able to colonize new areas (e.g., Richkus, 1978; Craik, 1981) . The rates at which juvenile and adult fishes colonize new habitat are of interest because the mobilities of different age classes are important in the dynamics of intertidal assemblages. In this report, we explore the recolonization, by juvenile and adult fishes, of tidepools following experimental removal of all fishes. Our work was conducted at a cold temperate northeast Pacific site where the intertidal ichthyofauna consists of about 12 abundant resident (sensu Cross, 1981) species and occasionally includes several transients from the adjacent subtidal (Chotkowski, 1994). More than 80% of the fishes found in tide-

pools at the site are sculpins (Cottidae) or pricklebacks (Stichaeidae); other abundant species include a clingfish (Gobiesocidae) and two kelpfishes (Clinidae).

Repeated collections in these tidepools were made to address three questions: (1) what is the time course of recovery of fish density and diversity; (2) which resident fishes most readily recolonize defaunated tidepools; (3) for abundant resident fishes, does the colonist source pool differ in size structure from the initial population? To distinguish postdefaunation colonization by juvenile and adult fishes from the natural turnover processes (i.e., recruitment), we hereafter refer to the replenishment of tidepool fishes after experimental removal from tidepools as "recolonization." Furthermore, "new colonists" are defined as species that appeared in tidepools in collections made after the initial defaunation but were not present in the initial collections.

MATERIALS AND METHODS

We made collections in tidepools at the Bodega Marine Reserve, Sonoma County, California (38°18'N, 123°3'W), from 5 October 1992 to 6 January 1993. We defaunated a fixed set of tidepools on one to three occasions, with an intercollection interval of 1-90 days separating successive collections. In most cases, we defaunated tidepools with rotenone, although a few tidepools were defaunated by bailing out the entire tidepool contents when size (volume) was not prohibitive. In rotenone collections, fishes were captured with dipnets until approximately 30 min passed without captures. At that time, we partially bailed the tidepools to facilitate a search for dead fishes. Collections obtained using rotenone in tandem with partial bailing are similar to collections obtained by complete bailing. Chotkowski (1994) partially or completely bailed 24 tidepools at BMR after they were treated with rotenone and reported to be completely collected. Tidepools that were not completely collected. Tidepools that were not com-

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pletely bailed were bailed until the water level was low enough to see the bottom. On average the total number of fishes taken from a pool was increased by 8.6% when bailing was used in addition to rotenone treatment. In none of the 24 cases was a species found during bailing that was not collected after rotenone treatment alone. Because this result indicates that the rotenone-only protocol we used yields similar results to collections obtained using rotenone and bailing, we treated all collections taken in the present study alike. Voucher specimens were deposited in the fish collection at the University of California, Los Angeles.

Seven tidepools were defaunated only once, 12 were defaunated twice, and four were defaunated three times. We assigned intercollection intervals to tidepools as follows: five tidepools had intervals of less than 10 days, seven tidepools had intervals of 10-20 days, five had intervals of 40-75 days, and seven had intervals of 80-91 days. Vertical elevation of tidepools relative to MLLW was estimated by use of tide gauge data obtained by the Bodega Marine Laboratory; elevations of sampled tidepools varied between 1.0 m below and 0.5 m above MLLW, but data are lacking for six tidepools.

We compared tidepool assemblages before and after defaunation using Schoener's (1968) proportional similarity index (PSI), which ranges between zero (no species shared by original and colonist assemblages) and unity (all species present in both assemblages and in similar proportions). Overall changes in density and Brillouin's (1962) diversity were compared between initial and second collections. We evaluated the "colonizing ability" of individual species by comparing the number of tidepools occupied by a species after the intercollection interval with the number occupied in the initial collections.

RESULTS

A total of 41 collections in 21 tidepools yielded 1240 fishes; collection results for abundant species are presented in Table IA. Table 1B shows, for the most abundant species, the number of individuals found in recolonist collections. Compared with initial collections, fish densities in defaunated tidepools were much lower in the first 20 days following defaunation than in the initial collections (Table 1; however, by 60 days postdefaunation, the mean fish density was not distinguishable from the -initial density (independent t-test, P < 0.05 by permutation; Fig. lA). Neither species richness nor Brillouin diversity differed between initial and second collections if the postdefaunation interval exceeded 60 days (species richnesses: P > 0.05 by permuted independent t-test; Brillouin diversities: P > 0.05 by Hutcheson's (1970) method; Fig. 1B).

The propensity of the most common species to recolonize tidepools was examined by comparing the rates at which those species occurred in both first and second collections across all collection intervals (Fig. 2). Over the entire range of intercollection intervals, the abundant cottids *C. analis*, *Artedius lateralis*, and *O. snyderi* and the stichaeid *Xiphister mucosus*, recolonized 61-91% of the tidepools they originally occupied; in contrast, the clinids *Gibbonsia metzi* and *G. montereyensis* recolonized 20-35% of their original pools, and the stichaeids *Cebidichthys violaceus* and *Xiphister atropurpureus* recolonized less than 22%. The proportion of tidepools recolonized by all species regressed significantly on the number of pools originally occupied (ß = 0.06, r^2 = 0.84, P < 0.024). Tidepools that were not occupied by a given species in initial collections tended not to be colonized by that species even after removal of the original fauna.

Colonist assemblages in individual tidepools tended to rapidly converge to the original assemblages (Fig. 3). Five tidepools resampled after intervals of less than 10 days had a mean PSI of 0.17 (compared with original fauna), whereas seven tidepools resampled after intervals of 80-91 days yielded a mean PSI of 0.70 relative to the original collection. At intermediate intercollection intervals, seven tidepools recollected after 10-20 days and five recollected after 40-75 days yielded similar mean PSIs of 0.39 and 0.48, respectively. The mean and extreme standard lengths of fishes obtained in second collections were compared with means and extremes obtained in first collections to determine whether, for each species, recolonists differ in size (age) distribution from the original tidepool occupants. Sample sizes of *A. lateralis, C. analis, O. snyderi, C. violaceus, X. atropurpureus, X. mucosus*, and the clinids *G. metzi* and *G. montereyensis* were sufficiently large (> 5) for analysis. Over all intercollection intervals, samples of the abundant cottids *C. analis* and *O. snyderi* had smaller mean and maximum standard lengths in second collections. This was due to an increase in the proportion of small, young-of-the-year individuals in the recolonist samples (P < 0.05; comparison of means by permuted independent t-test; Table 2). Because this study considered short intercollection intervals, this increase in young-of-the-year individuals clearly reflects the greater mobility of juve-

TABLE 1. (A) INITIAL COLLECTION RESULTS (IN NUMBER OF INDIVIDUALS) FOR ABUNDANT INTERTIDAL FISH SPECIES AT THE STUDY SITE. (B) Results of subsequent fish collections in tidepools where abundant species occurred (intercollection interval in parentheses following each tidepool name).

Tidepool	C. analis	O. snyderi	O. macul.	A. lateral.	C. glob.	X. mucos.	X. atrop.	C. viol.	G. metzi	G. mont.	Total
(A)											
1a	8	6	0	0	0	1	1	0	0	0	16
1b	7	1	0	0	0	3	0	0	0	0	1i
2a	3	3	0	0	2	0	1	0	0	0	9
2b	7	3	0	0	0	0	0	0	0	0	10
3a	0	13	0	6	1	3	0	0	5	3	31
3b	0	21	0	3	0	0	0	0	5	3	32
4a	0	7	0	5	0	0	3	0	0	2	17
5a	0	14	0	3	0	0	0	0	7	3	27
5b	1	3	0	4	0	0	0	0	6	1	15
6a	0	16	0	5	0	0	3	0	4	1	29
7a	0	6	0	11	0	0	0	0	5	0	22
8a	118	50	13	3	6	23	0	22	0	0	235
9a	13	25	0	13	0	1	0	0	0	0	52
10a	74	11	14	0	0	5	0	12	0	0	116
11a	2	8	1	0	11	1	2	0	0	0	25
12a	2	6	3	14	0	1	4	0	1	10	41
13a	24	18	7	0	1	4	0	4	0	0	58
14a	0	15	0	3	0	1	0	0	1	4	24
16a	8	11	3	5	1	7	7	2	1	2	47
17a	0	48	0	14	0	12	17	1	1	0	93
17b	0	38	0	12	0	3	0	0	22	6	81
(B)											
1a (8)	1	0	0	0	0	2	0	0	0	0	3
1b (8)	0	0	0	2	0	0	0	1	0	0	3
2a (14)	3	1	0	1	1	0	0	0	0	0	6
2b (14)	1	1	0	1	0	0	0	0	0	0	3
3a (15)	0	2	0	4	0	0	0	0	0	0	6
3b (15)	0	0	0	1	0	0	0	0	1	0	2
6a (15)	0	0	0	1	0	0	0	0	0	0	1
7a (1)	0	2	0	0	0	0	0	0	0	0	2
8a2 (14)	5	5	0	0	1	5	1	0	0	0	17
8a3 (71)	5	8	0	7	3	1	0	0	0	0	24
9a (91)	19	13	0	1	0	0	2	3	2	0	40
10a (98)	31	0	0	1	0	3	1	1	0	0	37
12a (72)	11	14	0	1	0	2	0	1	0	0	29
13a (90)	6	8	0	0	0	1	0	0	0	0	15
16a2 (11)	1	0	0	6	0	5	2	0	0	0	14
16a3 (73)	1	5	0	3	1	0	2	0	3	2	17
17a (72)	0	10	0	6	0	10	20	0	4	5	55
17b (72)	1	5	0	10	0	2	0	0	1	2	21

niles, rather than recruitment of neonates. No differences in sizes between initial tidepool occupants and recolonists occurred among the other six species.

Discussion

The apparently short composite restoration time (60-90 days to restore species richness, density, and Brillouin diversity) of this assemblage indicates that defaunated tidepools can be repopulated exclusively through colonization by an existing pool of juvenile and adult fishes rather than requiring recruitment of subsequent generations. The recolonization rate agrees with results from similar studies of intertidal fish assemblages (Beckley, 1985; Matson et al., 198'7; Mistry et al., 1989). The composition of the fish fauna remained dominated by the same species that were abundant in the initial collections, which agrees with the results of Grossman (1982, 1986) and
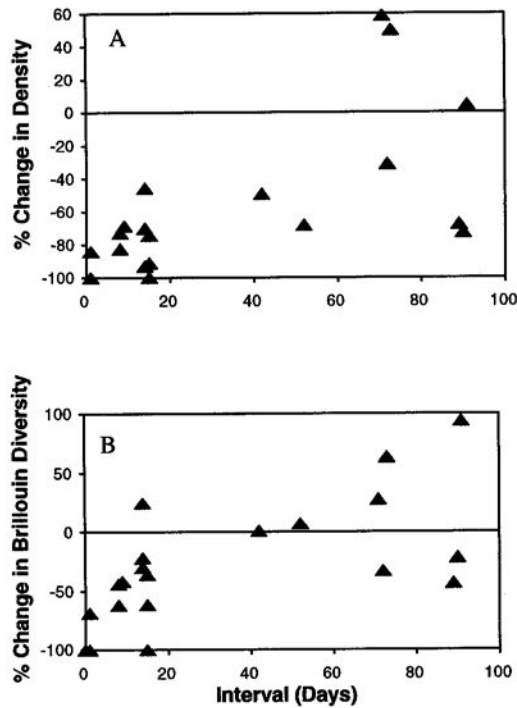
Fig. 1. Percent change in (A) fish density and (B) Brillouin species diversity between initial and postdefaunation collections for all intercollection intervals. For data points after 40–60 days, mean change in values did not differ significantly from zero ($P > 0.05$ by permuted independent t-test).

Fig. 2. Colonizing performance expressed as the proportion of tidepools occupied by species following defaunation. For each species, "recolonists" appeared in the same tidepools occupied by that species in the first collections, whereas "new colonist" species appeared in tidepools in which they were not originally present.

Mistry et al. (1989), but less abundant fishes appeared in initial and second collections at unpredictable levels. It is of further interest that *Chnocottus globeceps*, the most abundant species at the same study site six years prior to our study (Mistry et al., 1989) was found in relatively low abundance. This relatively large change in species abundance is an important indication that populations (at least for this species) undergo dramatic fluctuations in abundance over large temporal scales. Despite unpredictability in the appearance of less abundant fishes as "recolonists," the observed similarity in Brillouin diversity between initial and second collections after 40-60 days following defaunation indicated that the defaunated tidepools almost fully regained their previous species constituencies. Previous reports indicated that time intervals of 1-2 weeks (Mistry et al., 1989) and 45 days (Matson et al., 1987) were insufficient for recovery of defaunated tidepools, and our results indicate that original Brillouin diversities are approached 60-90 days after initial defaunations. Matson et al. (1987) found that Brillouin diversity did not recover after
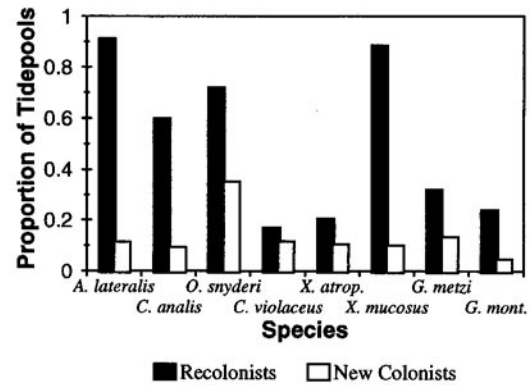
45 days at a sampling locality approximately 300 km south of our study site. At present, there are no known latitudinal differences in population dynamics that might account for the difference in restoration time between the two study sites. Application of the Brillouin index or one of the other diversity indices beyond the comparative context used here may not be appropriate for intertidal fishes of the northeast Pacific. The unpredictability of the occurrence of "rare" species is generally not incorporated into the Brillouin index. Tidepools with different rare species present in postdefaunation collections than in initial collections may be similar in Brillouin diversity but may have significantly different biotic
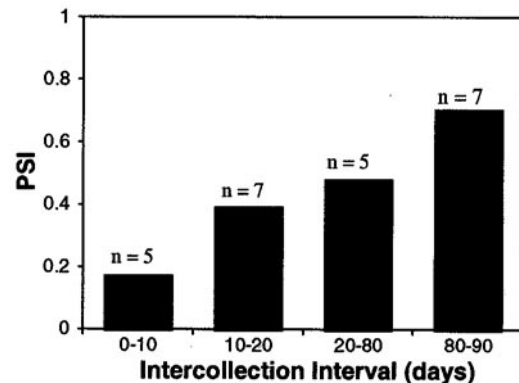

Fig. 3. Schoener's (1968) proportional similarity index between initial and second collections for all collection intervals. These PSI values, for the intercollection intervals are heterogeneous at $P < 0.03$ by the Kruskal-Wallis test.

TABLE 2. SIZE STRUCTURE OF RECOLONISTS. Results of permuted independent *t*-test for significant differences in mean SL between initial populations and recolonist populations of abundant resident intertidal fish species pooled over all intercollection intervals. Probability based on permuted independent *t*-test for equality of means (Edgington, 1987).

	Initial collection	Recolonist collection	Difference
Clinocottus analis	60.76 ± 4.01 mm	54.38 ± 1.86 mm	$P = 0.05$
Oligocottus snyderi	40.08 ± 1.43 mm	38.36 ± 1.56 mm	$P = 0.05$

interactions due to the presence or absence of a species that differs from the inital condition. More appropriate diversity indices account for species differences and apply taxonomic components to the measurement of importance within the assemblage (Cousins, 1991). Some diversity indices such as the Hill index deviate from their expected values when the relative proportion of one of the species involved is close to 1 (Gadagkar, 1989), but it is unknown whether this is also a property of the Brillouin index. Because samples in this study after short intercollection intervals are typically dominated by the earliest recolonist species, our use of the Brillouin index possibly underestimates the importance of the unpredictable, less abundant species. We employ the Brillouin index in this study to facilitate comparison with other studies (e.g., Matson et al., 1987).

The proportional similarity index was more instructive in reflecting the actual restoration of fish assemblage structure. The PSI accounted for the difference between initial and postdefaunation samples due to the less abundant species, and our PSI values can also be compared with those from studies in which fish assemblages have been studied for longterm stability or recovery following natural or experimental population reductions. Meffe and Sheldon (1990) experimentally defaunated various mesohabitats on five streams in the Savannah River drainage and found that assemblage recovery reached PSI = 0.7 after a one year postdefaunation interval (compared to 80 days in our study). Matthews et al. (1988) also reported high species similarities (at PSI = 0.6-0.8) between intercollection intervals of 5-15 years in two Ozark-Ouachita upland streams and one prairie-margin stream, which were followed over periods of natural fluctuations.

We observed taxonomic differences in recolonization propensity by tidepool fishes,

e.g., cottids tended to recolonize readily. We further suggest that our finding that the recolonists consist of greater numbers of smaller (juvenile) individuals (at least for *G. analis* and *O. snyderz*) may reflect the natural colonization process; that is, after settlement from the plankton into the intertidal zone, sculpins disperse among tidepools mainly during the juvenile stage. It is likely that adult individuals are much less available than juveniles to serve as recolonists for "newly opened" tidepools because larger fishes seem to show stronger localization behavior, at least for some species (Craik, 1981; Matson et al., 1986; Yoshiyama et al., 1992). In a recent study of three Oregonian intertidal cottids, Yoshiyama et al. (1992) suggested that home ranges possibly spanned several contiguous tidepools or surge channel areas. Consequently, observations of apparent recolonization of tidepools by large adult fishes may not necessarily represent actual changes in the home ranges of the fishes; they may merely reflect the routine movements of individuals within their home ranges.

No species showed a strong tendency to colonize tidepools in which it was not initially present, even after long periods of time following defaunation of tidepools. This could result either from an absence of potential colonists of that species in the area or from the lack of appropriate habitat or substrata in the tidepools. In any case, it appears that the recolonist fishes are selecting tidepools on the basis of properties that are unchanged by defaunation. Tidepools that a resident species occupied before initial collections were readily recolonized by individuals of the same species, whereas previously unoccupied tidepools were less prone to being colonized by that species. Stichaeids did not recolonize tidepools as readily as cottids and probably require more than 90 days to restore initial densities. Of the four stichaeids abundant at the site, only *X. mucosus* recolonized defaunated tidepools quickly. In a reciprocal transplant study of "homing" by *X. mucosus* at the same study site, most individuals departed from the pools into which they were transplanted, and one fish was found to have moved a distance of 50 m in 14 days; however, no individuals returned to their "home" tidepools (Polivka and R. Herzig, unpubl. data). Whether autecological features or biotic interactions result in the apparent higher mobility of *X.*

mucosus, relative to other stichaeids, is unknown.

In summary, the cottids *A. lateralis, C. analis,* and *O. snyderi* readily recolonized defaunated tidepools. Stichaeids, with the exception of *X. mucosus*, were slower to recolonize. For *C. analis* and *O. snyderi*, recolonists were, on average, smaller than the original occupants, consistent with previous reports that most intertidepool movements of intertidal fishes involve smaller, juvenile fishes (Gibson, 1967; Beckley, 1985).

ACKNOWLEDGMENTS

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