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Contribution No. 148 of the Catalina Marine Science Center.

Temporal and Spatial Variation in the Recruitment of the Sea Hare, *Aplysia californica*, at Santa Catalina Island, California

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Abstract — Recruitment of *Aplysia californica* was studied at Santa Catalina Island, California. *Aplysia californica* recruited almost exclusively to the red algae *Plocamium cartilagineum* and *Laurencia pacifica*. Monthly sampling of *Plocamium* revealed two peaks of recruitment in 1986: one in January and another in June. Recruitment varied between locations, with some sites having consistently more recruits than others. This variation in recruitment is expected to have important consequences for the dynamics of *A. californica* populations.

Introduction

Variation in recruitment can be an important factor structuring marine populations (Connell 1985; Gaines & Roughgarden 1985; Roughgarden *et al.* 1985). Variation in recruitment of sessile marine invertebrates has been relatively well studied (see Hawkins & Hartnoll 1982; Kendall *et al.* 1982; Keough 1983; Caffey 1985; Connell 1985; Gaines *et al.* 1985; Gaines & Roughgarden 1985; Wethey 1985). However, comparatively little work has been done on variation in the recruitment of mobile marine organisms (see Loosanoff 1964; Branch 1975; Underwood 1975; Sarver 1979; Bowman 1985) with the exception of reef fish (Eckert 1984; Jones 1984; Sale *et al.* 1984; Cowen 1985; Victor 1986). In addition to the obvious complication of their motility, the recruits of many mobile marine invertebrates are small and cryptic. As a result, there is often a gap of months to a year between actual settlement (defined as the point when an individual first takes up permanent residence on or near the substratum) and the first observation by the scientist (Branch 1975; Underwood 1975; Bowman & Lewis 1977; Watanabe 1984). This makes it difficult to separate the effects upon the adult population of settlement, post-settlement mortality and movement (Keough & Downes 1982; Connell 1985).

Studies of recruitment typically have found it to be highly variable, both between sites and between years: 1) sessile marine invertebrates (Hawkins & Hartnoll 1982; Kendall *et al.* 1982; Keough 1983; Caffey 1985; Gaines & Roughgarden 1985; Gaines *et al.* 1985; Hughes 1985; Wethey 1985); 2) starfishes (Loosanoff 1964); 3) gastropods (Branch 1975; Lewis & Bowman 1975; Underwood 1975; Bowman & Lewis 1977; Sarver 1979; Watanabe 1984; Bowman 1985); 4) reef fishes (Eckert 1984; Jones 1984; Sale *et al.* 1984; Cowen 1985; Victor 1986). This variation in recruitment often was crucial in structuring the adult populations under study. Here I report results of an investigation of variation in the recruitment of the sea hare *Aplysia californica*, an opisthobranch gastropod, at Santa Catalina Island, California. Recruits were found almost exclusively upon the red alga *Plocamium cartilagineum*. I show that recruitment to this alga varied both seasonally and between sites. This variation in recruitment would be expected to profoundly affect the ecology of this species, potentially producing variation in abundance, competition and age-structure from one year to the next, and from one location to another (Hughes 1984; Connell 1985; Roughgarden *et al.* 1985).

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Methods

The study was conducted near the Catalina Marine Science Center on the northern shore of Santa Catalina Island (33°27'N, 118°29'W). Figure 1 shows the location of the 11 sites mentioned in this paper. These sites were shallow (<10 m) rocky reefs, with > 50 % cover of foliose algae. Recruitment was monitored by counting the number of *Aplysia californica* present in weighed samples of algae. On each sampling date, up to 10 replicate samples of an alga were collected in the field from any one site and transported to the laboratory in plastic bags. I attempted to collect individual samples of algae which weighed approximately 100 g. In the laboratory, the algae was washed in fresh water, causing most of the *A. californica* to drop to the bottom of the container. The algae was then carefully searched for any remaining *A. californica*. I placed *A. californica* in sea water as soon as they were removed from the algae, and most were unharmed by their exposure to fresh water. Occasional individuals suffered osmotically-induced damage to the gill area; however, this did not appear to affect measurements of length. All *A. californica* found were measured to the nearest millimeter while in a relaxed posture (*i.e.*,neither balled up nor stretched out). To prevent serial correlation of the samples, a cutoff value of 2 cm was chosen to represent animals of less than 1 mo age post-metamorphosis (based on the laboratory growth curve in Kreigstein *et al.* 1974). Wet weight of the algae was recorded to the nearest gram. Data are presented as number of recruits/kg algae. Data were log(x+1) transformed before analysis; the figures show the untransformed data.

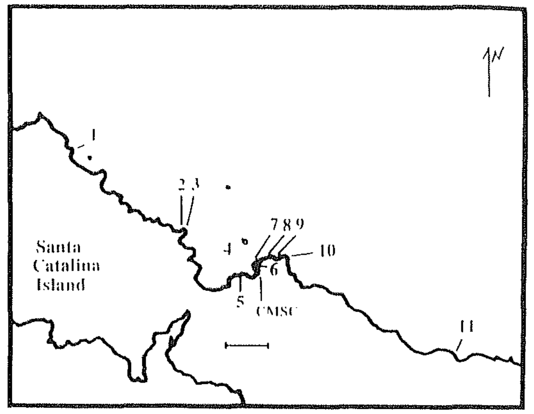

Figure 1. Map of the Two Harbors area of Santa Catalina Island, California, showing the location of the 11 sites sampled during this study. Bar = 1 km.

Recruitment to different species of algae was studied by collecting and searching, as described above, 9 species of algae from Site 4 in June, 1985. Data were analyzed using ANOVA. The temporal pattern of recruitment was studied by sampling *Plocamium cartilagineum* at Site 7 approximately monthly, from September, 1985 through February, 1987. This site was chosen early in the sampling program, and was later found to experience medium to low levels of recruitment (see Results). Data were analyzed using ANOVA. On five occasions, up to 10 sites were sampled simultaneously to yield information on spatial patterns of recruitment, and on whether these patterns were consistent over time. Data were analyzed using two-way ANOVA. The consistency of the ranks of the sites over time was examined using Friedman's test. Since Friedman's test does not allow for missing cells, I excluded the data from January 1987 and from Site 6, leaving nine sites which were all sampled on each of four dates.

Table 1. ANOVA tables for *Aplysia californica* recruitment: 1) recruitment to different species of algae (Fig. 2); 2) temporal pattern of recruitment (Fig. 3) and 3) spatial and temporal patterns of recruitment (Fig. 4).

Source	df	MS	*F*	Significance
Recruitment to different algae				
Species	8	16.97	86.76	P<.0001
Error	74	.20		
Temporal pattern of recruitment				
Date	14	9.52	7.90	P<.0001
Error	134	1.20		
Spatial and temporal patterns of recruitment				
Site	9	18.33	10.29	P<.0001
Date	4	104.92	58.93	P<.0001
Site x Date	32	6.04	3.39	P<.0001
Error	432	1.78		

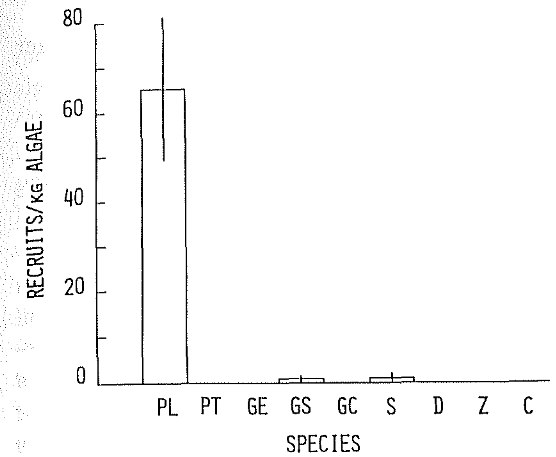

Figure 2. Recruitment of *Aplysia californica* to 9 species of algae at Site 4. Data are means with standard errors. Algal species were *Plocamium cartilagineum* (PL), *Pterocladia capillacea* (PT), *Gelidium robustum* (GE), *Gigartina spinosa* (GS), *G. canaliculata* (GC), *Sargassum muticum* (S), *Dictyota flabellata* (D), *Zonaria farlowii* (Z) and *Colpomenia* sp. (C).

Results

Aplysia californica recruits were found almost exclusively on the red alga *Plocamium cartilagineum*, and not on the other 8 species of algae sampled (Fig. 2; Table 1). Casual sampling of most other common species of algae at Santa Catalina Island produced few recruits and confirmed this pattern. *Laurencia pacifica* was the only other species of algae which consistently had recruits, and it was much rarer than *Plocamium* during the period of this study at all the sites I sampled. Small (< 2 cm) *A. californica* were never seen on bare rock or sand.

The number of *Aplysia californica* recruits per kg of *Plocamium* at Site 7 varied over time (Fig. 3; Table 1). There were two peaks of recruitment during 1986, one in January and the other in June, with a low level of recruits present year-round. The early peak of recruitment found in 1986 was not repeated in 1987, which suggests that there is year-to-year variability in the pattern of recruitment. Scattered observations from other sites at earlier dates also suggest that there is considerable year-to-year variation in the pattern and intensity of recruitment (S. Pennings, unpubl. data).

Sampling 10 sites on five dates revealed that the level of recruitment varied considerably in both space and time (Fig. 4; Table 1). The level of recruitment often varied more than an order of magnitude between high- and low-recruitment sites on any one date. In addition, the two-peak seasonal pattern of recruitment for 1986 found in the monthly sampling at Site 7 was corroborated. February and June 1986 had relatively high levels of recruitment overall, but April 1986 had relatively low levels of recruitment. In contrast to 1986, January

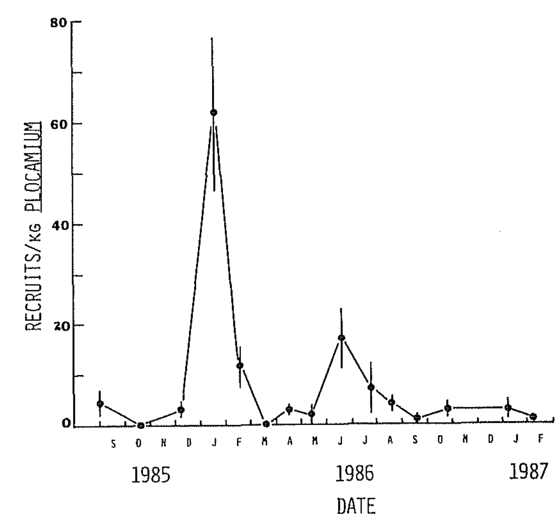

Figure 3. Temporal pattern of recruitment of *Aplysia californica* to *Plocamium cartilagineum* at Site 7. Data are means with standard errors.

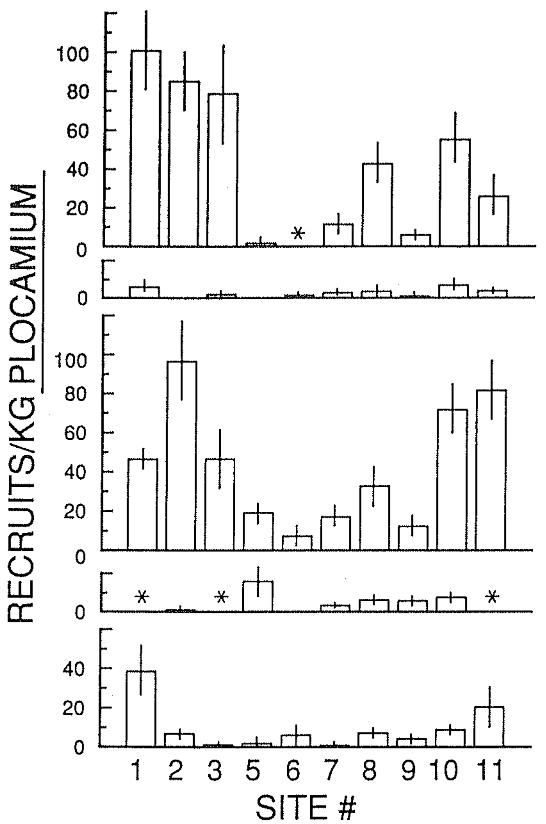

Figure 4. Recruitment of *Aplysia californica* to *Plocamium cartilagineum* at 10 sites on five dates. Data are means with standard errors. An asterisk represents sites which were not sampled on a particular date. Sites are plotted in geographical order from west to east. Dates, from top to bottom, are February, April and June 1986, and January and February 1987.

and February of 1987 had relatively low levels of recruitment. As noted above, this suggests that either the intensity or temporal pattern of recruitment is not consistent from year to year.

There was significant variation in the relative intensity of recruitment to different sites at different sampling dates (Table 1, Site x Date interaction). Despite this, Friedman's test showed that the ranks of the sites were significantly correlated over different dates (Fig. 5). Some sites were consistently ranked high; others were consistently ranked low. Consequently, despite a great deal of variation, some sites were predictably better than others for recruitment.

Discussion

The closer the time of observation is to the time of settlement, the more likely it is that one is observing settlement processes and not post-settlement mortality or movement. My samples contained recruits which I estimated, based on their size, to range from 1-4 wk post-metamorphosis. Ideally one would be able to sample individuals at the actual time of settlement; however, this study is an improvement over the lag of months between settlement and observation found in many gastropod studies (but see Sarver 1979; Bowman 1985). However, since there was still some lag between settlement and observation in my study, I cannot exclude the possibility that post-settlement mortality or movement may have been factors in the patterns I observed.

I found *Aplysia californica* recruits on *Plocamium cartilagineum* but not on the 8 other algal species I sampled (Fig. 2). I also observed recruits on the much rarer *Laurencia pacifica*. Kriegstein & co-authors (1974) reported that laboratory-reared *A. californica* would metamorphose only on *Laurencia pacifica* of 6 algal species tested, which suggested that *A. californica* had highly selective settlement behavior. Capo & co-authors (1979) subsequently reported that two red algae from New England also would induce settlement and metamorphosis. More recently, Pawlik (1989) reported very general settlement and metamorphosis of laboratory-reared *A. californica*, with some metamorphosis occurring on all of 18 algal species tested, although red algae were preferred. He suggested that *A. californica* might metamorphose on a variety of algae and then crawl to species which they prefer to eat. Whether *A. californica* settle selectively or generally in the field is not yet known, since the highly selective recruitment pattern I observed could have been caused either by selective settlement, or by general settlement followed by no growth or mortality on, or emigration from, algal species other than *Plocamium* and *Laurencia*. Although there are few rigorous studies of settlement preference in other *Aplysia* species, results are generally similar in that there seem to be some algae which are preferred, but settlement and metamorphosis is possible on a wider range of species (for review see Carefoot 1987).

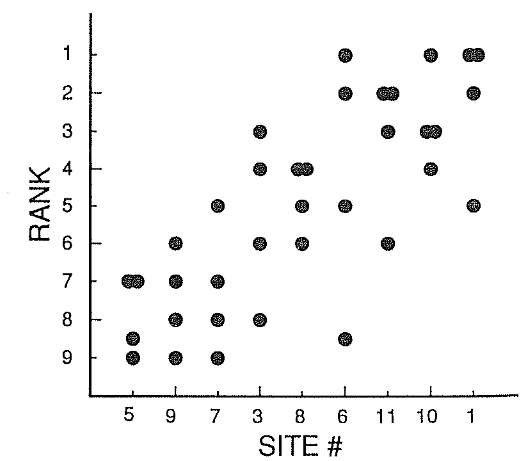

Figure 5. Ranks of 9 sites with respect to *Aplysia californica* recruitment on four dates. Sites are plotted in order of average rank, from consistently low-recruitment sites on the left to consistently high-recruitment sites on the right.

Sarver (1979) studied recruitment of *Aplysia juliana* to *Ulva* in Hawaii, and found that recruitment varied dramatically from week to week, from year to year, and from site to site. Those general results are similar to those reported here. I found that recruitment of *A. californica* varied greatly from month to month (Fig. 3), and from site to site (Fig. 4). In addition, there was a strong hint of year-to-year variation in the pattern of recruitment (Figs. 3 & 4).

Most other studies of *Aplysia* populations have examined larger animals some time after settlement. Audesirk (1979) studied *A. californica* weighing > 20 g (about 2 mo post-metamorphosis) at Santa Catalina Island. In 1973 and 1975, 20-100 g individuals were common from February-May, which suggests a January-February recruitment peak such as I found in 1986. In 1974, 20-100 g individuals were never common, suggesting a general failure of January-February recruitment such as I found in 1987. During all the years of Audesirk's study there was never a pulse of 20-100 g individuals during July-September. This suggests that a peak of recruitment in June, such as I found in 1986, either did not occur in those years, or that few of the recruits grew large enough to be sampled. Similarly, Carefoot (1967) presents size-frequency data for *A. punctata* in Anglesey, U.K., from July 1964-October 1965. 0-5 g individuals were most common from October 1964-January 1965, suggesting an autumn recruitment period. However, no small individuals at all were found in the autumn of 1965, suggesting that recruitment failed that year. Variable presence and abundance of adult *Aplysia* of a variety of species suggests that recruitment of *Aplysia* generally is seasonal and variable between years (see Carefoot 1987). In the same way, recruitment of other opisthobranchs rarely is studied directly, but variable recruitment can be inferred from temporally and spatially variable adult populations (Nybakken 1978; Todd 1981).

At Santa Catalina Island, reproduction of *Aplysia californica* peaks in July, August and September (Audesirk 1979; pers. obs.). Thus, there is at least a 4 mo gap between reproduction and recruitment. The larval period of *A. californica* is at least 34 days at 22° C in the laboratory (Kriegstein *et al.* 1974). Because development would be considerably slower in cold winter ocean water, it is conceivable that winter recruits to the island originated there from local reproduction. However, because no local peak of reproduction corresponds to the summer recruitment peak, it is likely that summer recruits to the island originate from populations elsewhere, and are brought to Santa Catalina Island by the regional current patterns (Cowen 1985).

Most studies of recruitment have found considerable spatial variation in its intensity (Bowman & Lewis 1977; Eckert 1984; Sale *et al.* 1984; Caffey 1985; Connell 1985; Gaines &

Roughgarden 1985; Victor 1986). Variation in settlement may be a function of: 1) larval supply to the site; 2) the ability of larvae to settle because of local physical conditions (such as turbulence) or 3) larval choice (Connell 1985). In some studies, some sites consistently have had more recruitment than others over time (Bowman & Lewis 1977; Kendall *et al.* 1982; Jones 1984; this study) (Fig. 5). In other studies, there was no consistent pattern over time of high- and low-recruitment sites (Williams & Sale 1981; Keough 1983; Eckert 1984; Caffey 1985). Explanation of these apparently contradictory results awaits more studies which are able to evaluate the roles of the above three mechanisms in determining settlement intensity (see Caffey 1982; Gaines *et al.* 1985). If some sites consistently rank higher than others in recruitment intensity, variation in recruitment may lead to consistent differences in other ecological processes such as growth and mortality between sites. The consistent site ranks found in this study (Fig. 5) suggest that *Aplysia californica* at different sites on Santa Catalina Island may experience consistently different ecological regimes. In particular, competition for preferred algal foods and the availbility of potential mates are two factors that are likely to consistently vary between high- and low-intensity recruitment sites.

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Contribution No. 131 of the Catalina Marine Science Center.

Geographic Variation in Population Characteristics of an Intertidal Gastropod: Demographic Differences or Settlement History?

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Abstract - Population characteristics of the littoral fringe periwinkle gastropod *Littorina keenae* were examined at two regions within its geographic range: Santa Catalina Island in southern California and Bodega Bay in northern California. Compared with Bodega Bay, populations at Santa Catalina Island were more dense and individuals had a smaller average body size. This pattern of latitudinal variation has been commonly observed among species of gastropods. Several lines of evidence suggest the pattern for *L. keenae* may be the result of settlement history and demography, and not caused primarily by genetic or phenotypic variation among regional populations. *Littorina keenae* was found to be a slow but variably growing, long-lived species with low per capita mortality. Mortality was independent of body size. No difference was found in growth rates between geographic regions. Females spawned thousands of planktonic egg capsules annually, but settlement of young appeared to be low and highly variable in time. Evidence suggests that settlement, when it occurs, tends to be spatially synchronous within a region but asynchronous among geographic areas. It appears that most local populations studied resulted from one (or a few closely timed) recruitment pulse(s). The interval between the last successful recruitment event appeared to be longer in the northern than southern region of California. This hypothesis was supported by a projection matrix model that simulated the frequency distribution of body sizes obtained in a local population under two extremes in temporal variability of recruitment: a single recruitment pulse and constant annual recruitment of the same magnitude. The results for the single recruitment pulse model matched well with observed population size structures.

Introduction

A commonly observed pattern among marine species is latitudinal variation in population characteristics. A typical pattern is for individuals at higher latitudes to have larger body sizes, reach older ages and have lower population densities than counterparts at lower latitudes. Such variation is prevalent among gastropod molluscs (*e.g.*, Newell 1964; Frank 1975; Fawcett 1984). While the pattern has been reported for a wide array of marine species, the underlying causal processes often remain unexplored.

There are several classes of mechanisms that can produce the latitudinal pattern described above. First, it can be genetically based, representing evolved adaptation to local conditions. Frank (1975) proposed the following scenario. Where reproductive success historically is uncertain and low, natural selection may have favored long-lived individuals. In turn, increased longevity may be made possible by a decreased reproductive effort per unit time. Conversely, where recruitment is high and predictable, selection may have favored adults that place maximal effort into making young, which is made possible by a lowered growth rate and reduced life span (*e.g.*, Murdoch 1966; Murphy 1968; Gadgil & Bossert 1970). Thus, for this mechanism to produce the observed geographic pattern, recruitment into populations must historically have been greater