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NOTE

Convergence in the time-space continuum: a predator-prey interaction

Ann L. Knowlton*, Raymond C. Highsmith

Institute of Marine Science, University of Alaska Fairbanks, PO Box 757220, Fairbanks, Alaska 99775-7220, USA

ABSTRACT: Predation is a key structuring mechanism for some marine communities. Prey abundances may fluctuate with strength of predator recruitment and persistence, except in cases where some of the prey population has a refuge in space or time from predation. The sponge *Halichondria panicea* is patchily distributed in the rocky intertidal on the south shore of Kachemak Bay, southcentral Alaska, and in certain locations is the spatial dominant. This long-lived sponge is dispersed by planktonic larvae. At one site *H. panicea* has dominated the mid-intertidal for at least 10 yr. Percent cover estimates show that *H. panicea* averaged 53.4 ± 9.9% cover from August 1994 through August 1996. A major predator on *H. panicea* is the nudibranch *Archidoris montereyensis*, which is also planktonically dispersed and has an annual life cycle. Predators with larval dispersal have the same obstacles to and potential for recruitment in suitable habitats as planktonically dispersed prey with the added constraint of locating within-habitat prey patches. Total numbers of *A. montereyensis* at the study site (550 m^2) ranged from 12 to 42 from 1994 to 1996. In the spring of 1997, strong recruitment resulted in an average population of 156 *A. montereyensis* on site from May to July. Percent cover of *H. panicea* declined from visual estimates of 40% in May to 15% in July. By August 1997, sponge was absent at the study site and the number of nudibranchs declined to 7 individuals by September. Even though *H. panicea* is abundant in the region and potential recruits should be numerous, as of June 1999, the site once dominated by *H. panicea* is open rock with heavy recruitment of annual macroalgae occurring. The predator-prey relationship of *A. montereyensis* and *H. panicea* is an example of a chase through space and time, with convergence resulting in extreme population fluctuations and an unstable community.

KEY WORDS: Predation · Nudibranch · Sponge · Intertidal · Predator/prey interaction · Community structure · Alaska · Recruitment

Community structure is influenced by many biotic and abiotic factors. Among the former, predation is a key structuring mechanism for some marine communities (Paine 1974). Prey abundances may fluctuate greatly with strength of predator recruitment and persistence, except in cases where some of the prey population has a refuge in space or time from predation. Consistent, moderate predation levels on a predictably available prey resource should lead to stable community structure with relatively small fluctuations in predator and prey population densities. Conversely, prey species lacking a refuge from predation are subject to major population fluctuations commensurate with variations in predator abundance.

Community stability can be attained when a prey species is capable of occupying a location (refuge) which its predators cannot occupy due to physiological or other constraints. There are a number of intertidal examples. Dense bands of the mussel *Mytilus californicus* occur in the intertidal zone of the US Pacific Northwest, just above the upper foraging limit of the predatory seastar *Pisaster ochraceous* (Paine 1966, 1974). Harpacticoid copepods of the genus *Tigriopus* utilize high-level tidepools to escape predators common in lower tidepools (Dethier 1980). The lady crab *Ovalipes ocellatus* is adapted to deep burial in sandy habitats, which provides refuge from a variety of predators, including other crab species (Barshaw & Able 1990). *Choromytilus chorus*, a mytilid mussel, escapes predatory snails by settling on filamentous macroalgae and growing until they are large enough to attain refuge in size from the predators (Moreno 1995).

Sponges are major components of many benthic communities such as coral reef systems (Hartman 1977), epifaunal assemblages of McMurdo Sound, Antarctica (Dayton et al 1974), and algal and seagrass communities (Fell & Lewandrowski 1981, Theede 1981). In many cases sponges occupy a significant amount of available substrate, but are not typically spatial dominants. Where sponges do dominate, it is often an assemblage rather than a single species that occupies the space. One example that contradicts both

*E-mail: ftalk@uaf.edu

generalities is in McMurdo Sound, Antarctica, where 18 species of sponges occupy 55.5% of the available space and 41.8% of the available space is accounted for by a single species (Dayton et al 1974). The Antarctic sponge community occurs in a physically stable, low-energy environment that appears to favor a poriferan-based community. We investigated the encrusting sponge *Halichondria panicea* in an unpredictable and relatively high-wave-energy environment, the rocky intertidal zone in southcentral Alaska.

Halichondria panicea is widely distributed and can be an important component of algal and seagrass communities with relatively small colonies encrusted on blades and shoots (Fell & Lewandrowski 1981, Theede 1981) or on shells and pebbles (authors' pers. obs.). Ecological and reproductive studies have been carried out on subtidal populations (Ivanova 1981, Barthel 1986, 1988, Witte et al. 1994) but few scientists have investigated *H. panicea* living in intertidal habitats (Palumbi 1984). *H. panicea* is patchily distributed in the rocky intertidal and, in certain locations in Kachemak Bay, is the spatial dominant. At one such site *H. panicea* dominated the mid-intertidal for at least 10 yr, with low densities of potential molluscan predators such as *Archidoris montereyensis*, *Katherina tunicata*, and *Diadora aspera* present (R.C.H. has taken class field trips to the site every year since 1984 to examine the sponge population and interactions with algae and predators). This study was initiated to determine how *H. panicea* maintained dominance at the site by investigating changes in percent cover over time, potential for clone formation, interactions with macroalgae, and predator impacts. We report here on spatial cover over a 4 yr period and impact of high predator (*A. montereyensis*) recruitment in 1 yr.

Materials and methods. ***Study site:*** The study was conducted at Outside Beach State Park, Seldovia, Alaska, near the University of Alaska's Kasitsna Bay Laboratory on the Kenai Peninsula (Fig. 1). The region is highly productive due to upwelled water from the Gulf of Alaska entering Kachemak Bay (Sambrotto & Lorenzen 1986). Strong tidal currents resulting from an extreme tidal range of about 8 m distribute nutrients and food. The study site is a horizontal section of semi-exposed, mid-level rocky intertidal beach approximately 55 × 10 m, dominated by the encrusting sponge *Halichondria panicea*. The beach is composed of many large boulders and exposed bedrock with the sponge covering the exposed upper surfaces of the rock (Fig. 2A). Few colonies were observed growing on the underhanging regions of the rocks. The dorid nudibranch *Archidoris montereyensis* commonly feeds on *H. panicea* at this site (Fig. 2B), as do other facultative sponge predators including *Katherina tunicata*, *Diadora aspera*, and *Henricia* spp. (A.L.K. pers. obs.).

Observations: *Halichondria panicea* abundance was measured from August 1994 through June 1999 in 10 permanent 0.25 m^2 quadrats (Fig. 2C,D). Areal coverage was estimated monthly April to August and bimonthly September to March using a quadrat frame with a string grid having 81 intersections. Point counts were recorded for each intersection to estimate species composition of primary space occupiers below the canopy. An additional ten and five 0.25 m^2 quadrats in August and September 1997, respectively, were thrown at random to supplement the permanent quadrat coverage estimates. Data were taken in 4 categories, *H. panicea*, macroalgae, open rock, and other, and histograms of percent cover were plotted. Only the *H. panicea* data will be presented here. A photographic record of the permanent quadrats and of the site in general was compiled for most sampling dates.

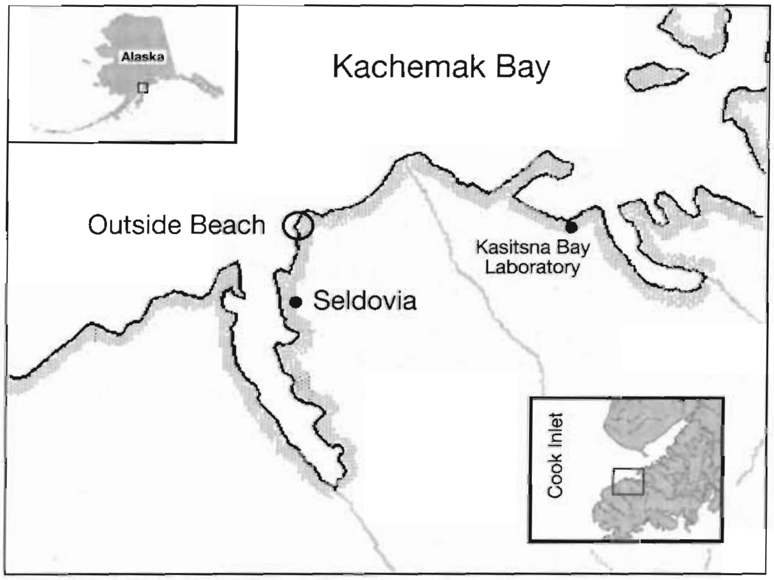

Fig. 1. Location of the study site at Outside Beach State Park (59° 28' 00" N, 151° 42' 06" W), near Seldovia, Alaska. Insets: regional context

The permanent quadrats were originally established to investigate the influence of algal canopy on *Halichondria panicea* abundance. Half of the quadrats were randomly chosen for removal of overlying macroalgae, while the remainder were untouched. Algal removal occurred in July 1994 and monthly April to July 1995. After July 1995 macroalgae were no longer removed and all quadrat flora were allowed to grow without ex-

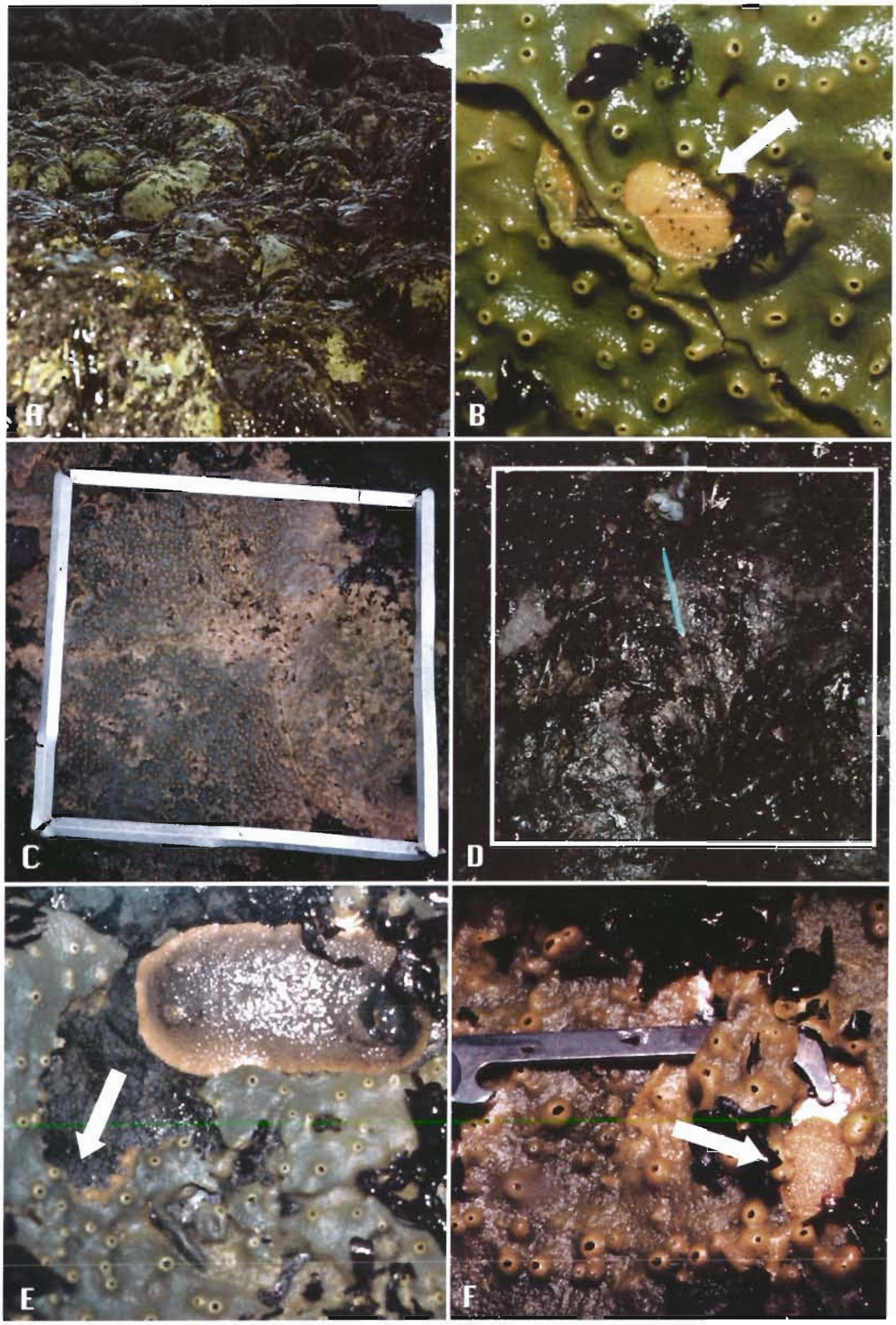

Fig. 2. (A) View of the study site in 1994 with numerous large colonies of *Halichondria panicea* evident. (B) The nudibranch *Archidoris montereyensis* (~25 mm long; arrow) burrowed into the sponge *H. panicea*. (C) One of ten 0.25 m^2 permanent quadrats in 1994 showing *H. panicea* dominance. (D) The same quadrat as in (C) in 1998 showing complete absence of sponge. Quadrat outline has been added for size reference. (E) A fresh feeding groove (arrow) made by *A. montereyensis* (~70 mm long). (F) A tunnel (indicated by the tool) created by a small nudibranch (~20 mm; arrow)

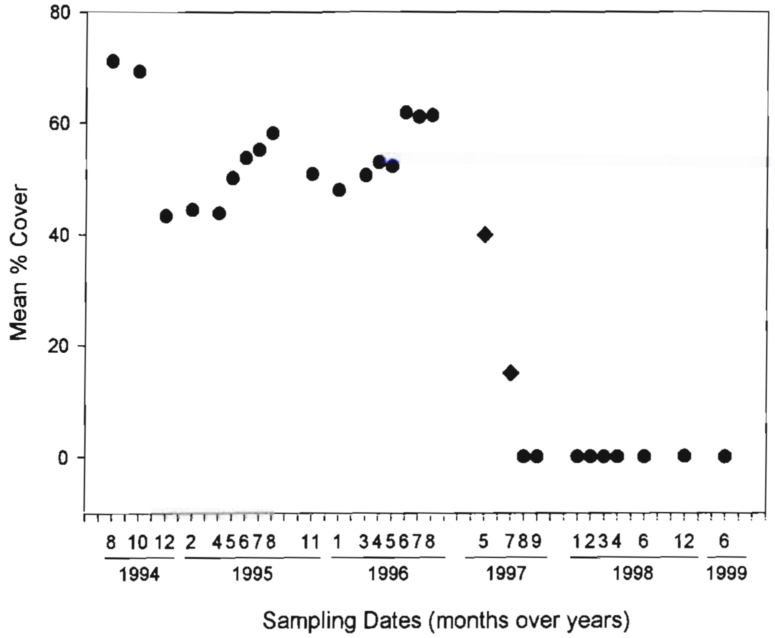

Fig. 3. *Halichondria panicea.* Mean percent cover at 10 permanent quadrats from August 1994 through June 1999. Points for May and July 1997 are based on visual estimates of percent sponge cover (◆). Data for 10 additional random quadrats in August 1997 and 5 in September 1997 are included. Numbers below *x*-axis denote sample month and year. Spaces between points represent months with no observations; width is not uniform

perimental intervention. Percent cover data collected from August 1994 to August 1996 were analyzed for treatment effects. A *t*-test of the slope of regression lines showed no significant difference ($\alpha = 0.05$) in *H. panicea* percent cover between treated and control quadrats, so data were pooled for the entire study period for analysis of predator impacts.

Archidoris montereyensis were counted and measured at the study site each July from 1994 to 1997, with additional counts in May, August, and September 1997, January through June 1998, and June 1999. Nudibranch body lengths were estimated by holding a plastic rule just above the animals without disturbing them. This method does not yield precise lengths, but is adequate for comparison of relative nudibranch sizes over time at a site.

Results. At the study site *Halichondria panicea* is not a cryptic species, but rather, occupies upper surfaces of boulders (Fig. 2A) usually colonized by barnacles, mussels, or algae. Average *H. panicea* cover was 53.4 ± 9.9% through fall of 1996 (Fig. 3). Visits to the site in early spring 1997 revealed that the sponge colonies overwintered with few indications of major mortality events, although percent cover data were not collected at that time as the original cover study had concluded. During subsequent site visits in 1997, visual estimates of *H. panicea* percent cover declined from 40% in May to 15% in July. By August 1997, when 10 permanent quadrats and 10 haphazardly placed quadrats were censused, only rock surfaces and algae were found (Fig. 2D). Just a single sponge colony was found at the entire study site. Through June 1999, no *H. panicea* were located within the permanent quadrats. Three small colonies were located on site amongst the holdfasts of the ribbon kelp *Alaria marginata* during the summer of 1998, but have subsequently disappeared.

Table 1. *Archidoris montereyensis* abundance and size-frequency distribution, 1994 to 1999. Nudibranch lengths were estimated to the nearest millimeter

Date		Number by size category (mm)							
	Total	<10	10–19	20–29	30–39	40–49	50–59	60–69	70+
Jul 1994	27	0	0	1	6	7	9	2	2
Jul 1995	42	0	0	3	12	10	9	5	3
Jul 1996	12	0	1	1	3	2	4	0	1
May 1997	177	0	6	30	52	64	20	4	1
Jul 1997	135	0	0	2	17	24	28	34	30
Aug 1997	32	0	0	0	6	9	10	5	2
Sep 1997	7	0	0	0	1	6	0	0	0
Nov 1997	2	0	0	1	0	1	0	0	0
Jan 1998	0	0	0	0	0	0	0	0	0
Feb 1998	2	1	0	1	0	0	0	0	0
Mar 1998	1	0	0	1	0	0	0	0	0
Apr 1998	1	0	0	0	1	0	0	0	0
Jun 1998	0	0	0	0	0	0	0	0	0
Jun 1999	0	0	0	0	0	0	0	0	0

The nudibranch *Archidoris montereyensis* is a specialized predator on *Halichondria panicea* (Bloom 1976) and is generally found aggregated on or near its sponge prey. We have searched many beaches within a few kilometers of the study site for other sponge-dominated locations and the presence of *A. montereyensis*. Occasionally a lone nudibranch will be found that is not near *H. panicea*, but most are found in pairs feeding on the sponge or producing gelatinous egg ribbons adjacent to sponges. Adult *A. montereyensis* are relatively easy to observe because of their yellow color, presence of egg ribbons, and grazed-out feeding tracks in the sponge colony (Fig. 2E). In thicker portions of colonies, the nudibranch feeding grooves may turn into tunnels (Fig. 2F) that presumably result in undermining the attachment of the colony to the rock surface. As nudibranchs creep on a large foot also adapted for attachment, they are not very mobile and are unlikely to migrate any appreciable distance, especially between boulders separated by unstable gravel (Fig. 2A). Therefore, the aggregation of *A. montereyensis* individuals with *H. panicea* is likely due to selective settlement of the nudibranch larvae in response to a chemical cue produced by or associated with the sponge, which they feed upon preferentially (Bloom 1976).

Although it has been stated that *Archidoris montereyensis* larvae settle within 2 h of hatching (Morris et al 1980), we agree with Strathmann (1987) that such rapid settlement is unlikely. The mean *A. montereyensis* egg diameter given in Strathmann (1987) is 81.5 µm. For eggs preserved 24 h after deposition, we found a mean diameter of 88.5 ± 13.9 µm (n = 25, range 75 to 125 µm). Such small eggs suggest planktotrophic development rather than direct development with immediate post-hatching settlement. This view is further supported by Hurst's (1967) data. *A. montereyensis* larvae probably feed and disperse over a period of several days to a few weeks.

Total numbers of the nudibranch *Archidoris montereyensis* present at the site ranged from 12 to 42 from 1994 to 1996 (Table 1, Fig. 4A). Strong recruitment in 1997 resulted in an average population of 156 *A. montereyensis* on site from May to July (Fig. 4B). Because of the low numbers of individuals on site in 1996, high winter survival is not a likely explanation of the increase in nudibranch numbers in 1997. A regression of monthly mean nudibranch length for 1997 suggests a recruitment event occurred early in 1997 (Fig. 4C). After July, the abundance of nudibranchs declined to 32 individuals, commensurate with sponge reduction (Fig. 4B). By September, only 1 small sponge colony and 7 nudibranchs were present at the site. From January through June 1998, very few nudibranchs were observed and were not in the vicinity of the few remaining *Halichondria panicea* colonies. These individuals were possibly feeding upon alternative prey or small, cryptic colonies of *H. panicea* that we did not notice. Since 1998 through July 1999, no nudibranchs have been seen at the study site.

The study site is on a semi-exposed rocky intertidal shore (Fig. 2A), more exposed than where one would expect to find 10s to 100s of nudibranchs aggregated. We postulate that the sponge colonies being preyed

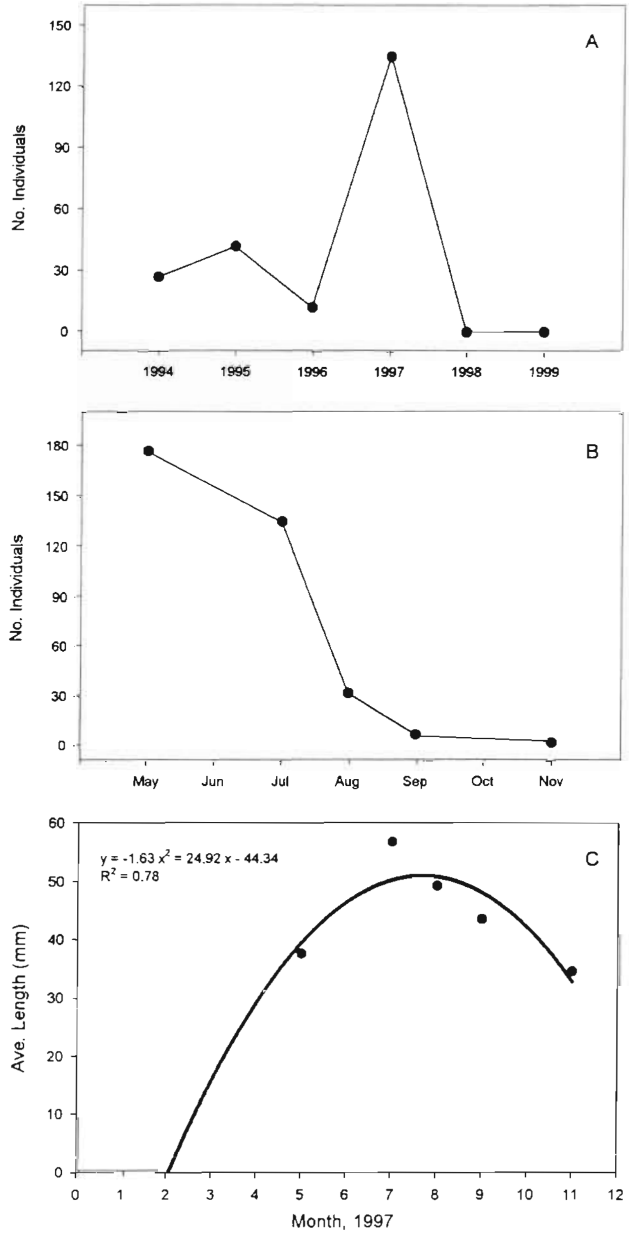

Fig. 4. *Archidoris montereyensis* population characteristics. (A) Annual census 1994 to 1999 taken each July (1998 and 1999 censuses taken in June). (B) May to November 1997 counts. (C) Regression of nudibranch mean lengths over time in 1997. Numbers below *x*-axis denote calendar month

upon provide shelter for the nudibranchs which occur around the edges of colonies and in grooves and tunnels grazed in the sponges (Fig. 2B,E,F), all of which reduce drag forces. When the sponges are removed, the nudibranchs are probably much more susceptible to removal by wave action. Also, the sponge colonies are probably more susceptible to wave removal due to grazing impacts and resident nudibranchs may be carried away with them.

Discussion. The intertidal sponge *Halichondria panicea* apparently relies on a patchy, unpredictable distribution, both spatially and temporally, as a refuge from its major predator. This system is similar to the predator-prey relationship found for the sea pen *Ptilosarcus gurneyi* and its main predator *Mediaster aequalis* (Birkeland 1974), in which both species utilize planktonic larvae for dispersal. While community dynamics and compositions differ between the rocky intertidal inhabited by *H. panicea* and the sandy subtidal habitats occupied by *P. gurneyi*, the mechanisms that appear to structure the communities are the same. A key prey species, also termed 'key-industry species' (Elton 1947), can shape an entire community, determining species composition, abundance and stability over time. At our study site in Kachemak Bay, *H. panicea* was the key-industry species for over a decade. Even though it is abundant in the region and potential recruits should be numerous, as of June 1999, the site once dominated by *H. panicea* is open rock with heavy recruitment of annual macroalgae occurring. The community is undergoing a restructuring brought about by the removal of the dominant space occupier by its primary predator.

Over evolutionary time, predators must adapt to changes in the defense mechanisms of their preferred prey, remain a generalist, or go extinct. Many studies have focused on predators modifying behaviors or life-history strategies as their prey species develop new chemical and morphological defense mechanisms or find new refugia (Birkeland et al 1971, Bloom 1976, Vermeij 1987). In cases where prey are patchily distributed in habitats in which predators are not physiologically or otherwise excluded, and the major predator has limited adult mobility, then the patchy, unpredictable location of the prey may serve as a refuge. The random distribution of prey populations within a habitat is a result of larval dispersal by currents. In some years and locations, recruitment may be high due to favorable planktonic conditions, current patterns, and availability of a suitable site, perhaps due to a recent disturbance that removed resident species. Predators with larval dispersal have the same obstacles to and potentials for successful recruitment in suitable habitats with the added constraint of locating within-habitat prey patches. High predator recruitment may occur when all requisite conditions are met and the larvae detect cues indicative of prey presence (Mauzey et al 1968, Birkeland et al 1971, Birkeland 1974). In this case, a refuge site is lost as both prey and predator eventually become locally extinct at the site. This type of system may provide long-term, large-scale stability to a species but only short-term stability to a population at a given location. The predator-prey relationship of *Archidoris montereyensis* and *Halichondria panicea* is an example of a chase through space and time, with convergence resulting in extreme population fluctuations and an unstable community.

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