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A seventeen-year study of the rose star *Crossaster papposus* population in a coastal bay in southeast Alaska

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Abstract A 17 yr study of a population of the rose star *Crossaster papposus* (Linnaeus, 1767) in Auke Bay, near Juneau, Alaska, used SCUBA to follow a total of 956 individually marked stars. Population density was relatively constant over the 17 yr of study, although the influx of smaller individuals varied by an order of magnitude. Growth in diameter of individual stars was inversely related to size, with the largest individuals showing negligible growth for periods of months or years. Annual survivorship was relatively high (from 76.3 to 90.4%), and some individuals persisted throughout the study, indicating longevities of at least 20 yr in this species. Observations of food habits indicated that the principal prey item is the reddish scallop *Chlamys rubida*. In summary, this rose star population was characterized by a relatively stable number of long-lived, slow-growing individuals.

Introduction

Many invertebrates are rapidly responding, tractable subjects for life-history comparisons (Levin et al. 1987) and for understanding responses to natural disturbance (Paine and Levin 1981; Farrell 1991) and human-caused perturbations (Grassle and Grassle 1974; Castilla and Duran 1985). They are often highly abundant, and

dominate local areas; observations and manipulations of their numbers have provided insight into population dynamics and community-level pattern formation on relatively short time-scales (Connell 1961; Sutherland 1974; Paine 1980; Gaines and Roughgarden 1985; Wootton 1993, 1994). As a result, the majority of demographic information on marine invertebrates has come from species that are relatively fast-growing and short-lived.

There are a number of species that are members of nearshore marine ecosystems whose demography and life-history attributes remain little known. For long-lived species who are members of higher trophic levels (sea stars, cephalopods, decapod crustaceans), the relative paucity of their numbers and the longevity of individuals requires a long-term commitment in order to understand their life cycle. Consequently, we have long-term demographic information mostly for those species which are commercially exploited (e.g. lobsters: Wahle and Steneck 1991). Understanding the demography of many invertebrates is further complicated by their mobility. Not only is it difficult to gather demographic information on mobile or migratory individuals, but individual movement often makes it difficult to determine the boundaries of populations and to judge the relative constancy of individual numbers.

This study was conducted on the rose star *Crossaster papposus* (Linnaeus, 1767), family Solasteridae. Although it is a conspicuous and ubiquitous star of northern seas, documented observations of it in nature are rare. It is circumpolar, and is found in all northern seas from subtidal to oceanic depths (D'yakanov 1968). The identity and persistence of individuals at a specific site are virtually unknown, as are related aspects of their biology such as growth, migration, recruitment, survivorship and longevity. The rose star is often bright red and white, has 8 to 16 arms (usually 11), and reaches 34 cm in diameter (Lambert 1981). It feeds mainly on other asteroids and bivalves in British waters (Hancock 1974) and the North Atlantic Ocean (Mortensen 1977),

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and on sea pens and nudibranchs in the Puget Sound region of Washington state (Mauzey et al. 1968). Laboratory studies have shown that rose stars have a chemoreceptive ability to detect food and predators at a distance (Sloan and Northway 1982).

The reproductive cycle of *Crossaster papposus* includes peak spawning during March to April in Puget Sound (Strathmann 1987) and Scottish waters (Lambert 1981). Sexes are separate, and release gametes into the water. The large, buoyant, yolky eggs develop into nonfeeding pelagic larvae. From the time of egg release, development to an 11 mm juvenile with nine arms takes place in 47 d in Puget Sound (Strathmann 1987). Individual stars are agonistic, avoiding contact with conspecifics in the laboratory (Sloan 1984; corroborated by the present study).

In this study, we analyzed 17 yr of mark-recapture data for 956 individuals of the rose star *Crossaster papposus* in Auke Bay, Alaska. We used these data to estimate individual growth rates, annual survivorship probabilities, recruitment and migration into the population, and fluctuations in population abundance over time. Additionally, we used feeding observations to determine the trophic role of *C. papposus* in Auke Bay.

Materials and methods

The study was conducted in Auke Bay, Alaska (58°22'N; 134°40'W), one of many small embayments of a system of large fjords connected with the open ocean. The Bay is 130 km from the open coast; it covers ≈ 11 km², with 40 to 60 m depths common, and has a maximum depth of 100 m (Bruce et al. 1977). In Auke Bay, Alaska, *Crossaster papposus* (Linnaeus, 1767) occurs at depths from 10 m to >40 m.

All underwater observations and data collection were made by one of us (HRC), totalling 1525 dives from 1980 to 1997. Censusing effort was distributed relatively equally throughout all months of the year, with an average of seven dive-days per month and 86 d per year. The underwater transects focused on two prominent rocky ledges (described by Carlson 1995) which parallel the shore and extend for 240 m in Auke Bay. Surveys were made in daylight and in darkness, and covered depths from the subtidal down to 40 m. Routine searches were made outside the survey area (within a 15 km radius) to locate any marked stars that might have left the study area. Searches were conducted at least monthly in immediately adjacent areas, seasonally at other Auke Bay sites, and yearly in nearby waters.

Rose stars were collected by hand, usually one to a few at a time, and were held for a few hours to 1 wk in a circulating-seawater tank or in a mesh bag at subtidal depth until they were marked. Early in the study it became apparent that some stars remained at the site, and thereafter all unmarked stars sighted there were collected and marked. The smallest stars (<5 cm) were later excluded from collecting and marking because their cryptic behavior made them difficult to resight. For marking, excess water was blotted off, and neutral red dye was applied with a small paintbrush around the arm base or tip. The dye set within 2 to 3 min and normally lasted 3 to 5 yr in a distinctive, readable state. Nearly all rose stars in this study had 11 arms; one star had 14, and a few had 12, 10 or, rarely, fewer. The marking system used the madreporite (located between two arms) as a reference point, and was undertaken clockwise. The first arm clockwise from the madreporite was designated No. 1; the subsequent eight arms (clockwise) were successively numbered 2 to 9. Identification marks were designated as follows: 1 to 9, individuals marked at base only of Arms 1 to 9, respectively; 10, 20, 30,... etc., individuals marked at tip only of Arm 1, 2 or 3, respectively, etc.; 12, 23,... etc., individuals marked at tip of Arm 1 and base of Arm 2, or at tip of Arm 2 and base of Arm 3, respectively, etc.; >99, one or both of Arms 10 and 11 marked at base or tip for each series of 100. Rose Star No. 425 is shown as an example: end number "5" indicates dye mark at base of fifth arm, "2" indicates mark at tip of second arm, and "4" indicates that Arms 10 and 11 were marked in accordance with marking system adopted for Series 400, i.e. marks at both bases and tips

23,... etc., individuals marked at tip of Arm 1 and base of Arm 2, or at tip of Arm 2 and base of Arm 3, respectively, etc.; >99, one or both of Arms 10 and 11 were marked at base or tip for each series of 100. As an example, Fig. 1 shows a rose star with the identification number 425: the end number "5" indicates a dye mark at the base of the fifth arm, "2" indicates a mark at the tip of the second arm, and "4" that Arms 10 and 11 were marked in accordance with the marking system adopted for Series 400, i.e. marks at both bases and tips. When a mark faded, the star was collected again and re-marked. Few stars reacted adversely to the marking process. Thermal distress on warm days was the only problem, and this was minimized by holding stars at ambient subtidal sea temperature until they were marked, and then releasing them in the center of the study area at the approximate collection depth as soon as the dye had set.

Size was measured as maximum star diameter (mm), because missing or truncated arms were common. Growth was estimated as the change in diameter. Diameter was not measured regularly; most individuals were sized only when they were initially marked, and

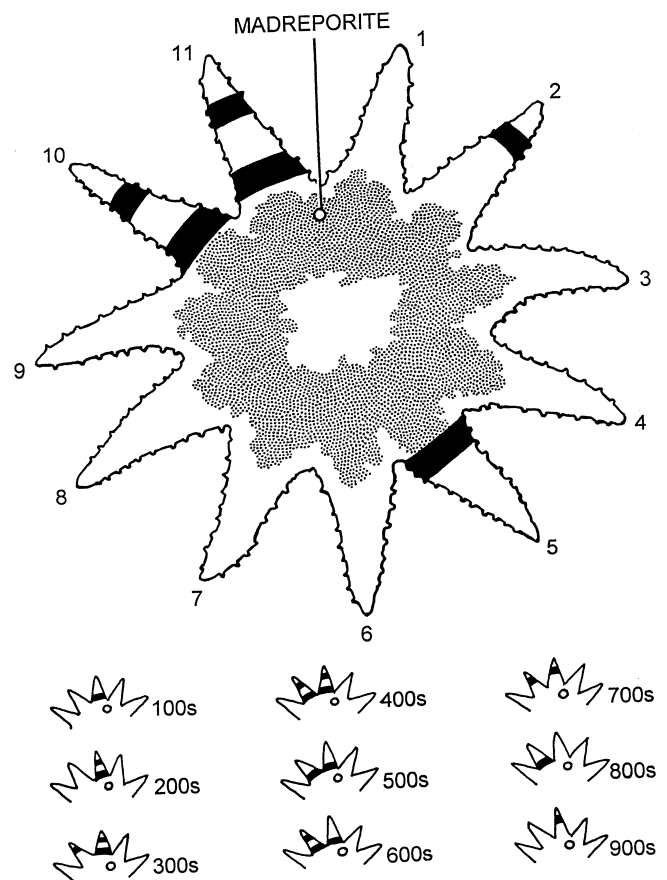


Fig. 1 Marking technique for rose stars, *Crossaster papposus*. Rose stars usually have 11 arms. The marking system used the madreporite (located between two arms) as a reference point, and was undertaken clockwise. First arm clockwise from madreporite was designated No. 1; the subsequent eight arms (clockwise) were successively numbered 2 to 9. Identification marks were designated as follows: 1 to 9, individuals marked at base only of Arms 1 to 9, respectively; 10, 20, 30,... etc., individuals marked at tip only of Arm 1, 2 or 3, respectively, etc.; 12, 23,... etc., individuals marked at tip of Arm 1 and base of Arm 2, or at tip of Arm 2 and base of Arm 3, respectively, etc.; >99, one or both of Arms 10 and 11 marked at base or tip for each series of 100. Rose Star No. 425 is shown as an example: end number "5" indicates dye mark at base of fifth arm, "2" indicates mark at tip of second arm, and "4" indicates that Arms 10 and 11 were marked in accordance with marking system adopted for Series 400, i.e. marks at both bases and tips

again several years later when they needed to be remarked. We examined if individual growth rates were positively correlated through time, indicating that individuals that were identified as fast growers early in the study remained so throughout the study. When the size of an individual was recorded at least three times, we estimated the growth rate in the first interval and the second interval and examined the Spearman correlation coefficient of the two growth estimates.

We estimated the annual survivorship probability from the number of resightings of individual sea stars using two methods: the Ricker (1958) method and an actuarial method described by Norman and Streiner (1994). Because the two methods differ slightly in how they use the available data, we report both survivorship estimates. The Ricker method quantifies the decline in the number of resightings over time. We first estimated the regression coefficient for the relationship between the natural log of the number of resightings and the years elapsed for individuals newly marked in each year of the study. The antilog of the regression coefficient for each year provides the annual survivorship probability. Thus, we estimated annual survivorship for individuals marked from 1980 through 1995, generating 16 independent estimates of annual survivorship. There was insufficient time to resight individuals marked in 1996 and 1997, and so these years could not be included. Since the number of individuals newly marked in any given year was variable (14 to 96), we used weighted regression to estimate a weighted mean and standard deviation for annual survivorship using the Ricker method (Sokal and Rohlf 1995).

An alternative method for estimating survivorship that also allows the inclusion of all the information from individual markings and resightings is an actuarial method (Norman and Streiner 1994). This method differs from the Ricker method by accounting for individuals who are "censored" (or still remain) at the end of the data analysis in 1997. Both methods are valid, and allow an estimate of the probability that an individual is still alive any number of years after it was initially marked.

We estimated the size of population over the course of the study in two ways: (1) we estimated population size as the number of individuals that were sighted in any given year, both as a simple count and normalized to the number of dive-days in that year; (2) we incorporated the observation that some individuals disappeared for several years (presumably migrating to deep areas out of the depth range of conventional SCUBA) and then reappeared in a subsequent census. We thus counted individuals as present in any given year if they reappeared in any subsequent census. In summary, the first estimate indicates the number of individuals at < 40 m depth at our study site in Auke Bay in any given year, while the second provides an estimate of total population size utilizing our study site.

We used the appearance of unmarked individuals in the population to provide an estimate of the yearly recruitment of small individuals and the immigration of larger individuals. We arbitrarily divided the population into a group of smaller individuals (≤ 100 mm diam) that might represent some estimate of recent recruitment, while larger individuals (> 100 mm) were designated as immigrants.

The diet of rose stars was quantified from 369 observations of individual feeding events. During all censuses, all rose stars that were encountered were turned over to examine the lighter, oral side where the dye marks contrast; any food items were noted. Small items not readily identified underwater were collected for positive identification.

Results

Growth rate

The growth rate of *Crossaster papposus* was negatively related to increasing diameter (Fig. 2), and averaged 11.2 mm yr^{-1} (± 7.3 SD) over all 207 individuals mea-

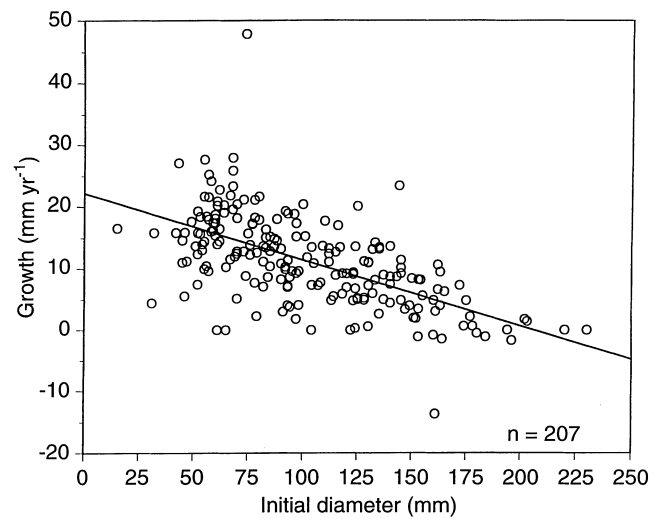


Fig. 2 *Crossaster papposus*. Growth as a function of initial diameter. Size explained a significant amount of variation in growth, with a linear regression (growth = $22.1803 - 0.1078$ size, $r^2 = 0.372$, $p < 0.001$, $n = 207$). Average interval used to estimate growth was 4.15 yr

sured. Size (mm diam) explained 37.2% of the variation in growth rate, a statistically significant amount ($p < 0.001$). If the outlier in the upper quadrant of Fig. 2 is removed, the p value remains at < 0.001 , and the variation that size explains increases to 40.0%. Thus, larger stars often showed little or no change in size. As further evidence for slow growth, arms lost or truncated took years to regenerate. A medium-sized star (126 mm diam), with an arm severed at the base and an arm cut in half, took 4 yr to regenerate the former to half its original length and to completely regrow the latter. A large star (236 mm diam) with two arms severed at the base took nearly 9 yr to regrow both arms to three-quarters their original size.

Twelve individuals were resighted and remeasured at least four times over a period of 8 yr or more, enabling us to track their individual growth trajectories for almost 17 yr (Fig. 3). The diameter of most individuals appeared to reach a maximum near 180 to 200 mm. During the 17 yr study, no individual exceeded 237 mm.

There was no evidence that individual growth rates were correlated through time ($r = -0.149$, $p = 0.269$, $n = 57$). Rose stars may reach their maximum size asymptotically (Fig. 3); therefore we also estimated the correlation for smaller individuals (≤ 100 mm) that might have been growing continuously throughout the study period. Again, there was no significant correlation during the first and second intervals when growth was estimated ($r = -0.229$, $p = 0.161$, $n = 39$). Thus, these analyses suggest that growth rates of individuals are relatively independent over time, and that the variability in growth rates (Fig. 2) did not result from consistent disparities among individuals.

Unfortunately, it was difficult to estimate size and age relationships for the cryptic, small individuals < 50 mm;

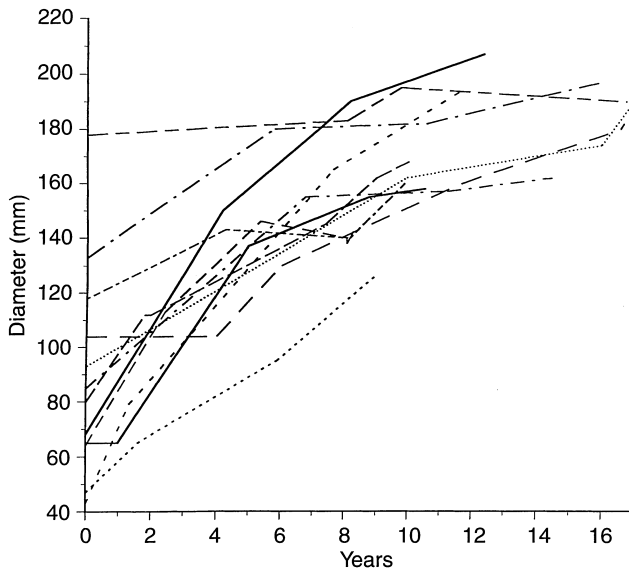


Fig. 3 *Crossaster papposus*. Individual size trajectories for 12 individuals resighted at least four times over 8 yr

however, there is evidence from newly-settled *Crossaster papposus* maintained in the laboratory that individuals ≥ 40 mm are in their second year (HRC personal observation). To determine the range of size and age relationships, we used the equation in the legend to Fig. 2 to project the size of individuals, starting with a 2 yr-old at 40 mm. We used the mean estimated y -intercept and slope, as well as the values obtained from subtracting or adding the 95% confidence limits of these estimates, resulting in nine possible combinations of the y -intercept and slope. Fig. 4 shows possible relationships between size and age. Although there is some uncertainty in the age of larger individuals, it is highly likely that individuals > 160 mm are at least 20 yr of age.

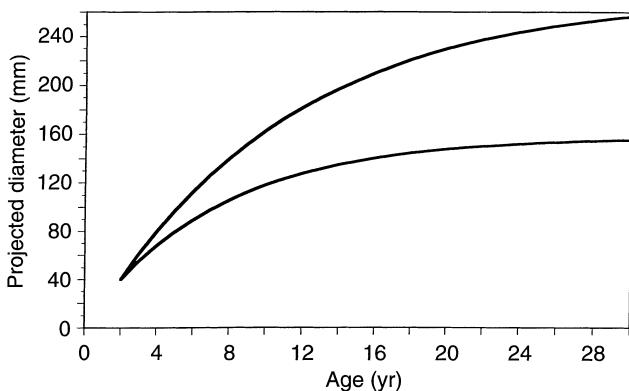


Fig. 4 *Crossaster papposus*. Size and age relationships based on projected size of 40 mm individual in Year 2, using regression equation in legend to Fig. 2. Area within and including curves represents range of relationships between size and age when 95% confidence intervals are included in slope and y -intercept

Survivorship

Of a total of 956 rose stars that were marked and released during the study, 86% were sighted at least once following release. The annual survivorship probability estimated from the Ricker method was 0.763 ± 0.085 (weighted mean and standard deviation), ranging from 0.540 to 0.847 over the 16 yearly cohorts available for analysis. Estimates of mean annual survival based on an actuarial method were greater (0.904 ± 0.109 SD), ranging from a low value of 0.533 in the first year following marking to 0.988 in the sixteenth year after marking. Thus, the probability that an individual marked in the first year of the study would still be present 17 yr later was 0.010 with the Ricker method (using an annual average) compared with 0.155 with the actuarial method (using a cumulative probability). Obviously, both survivorship estimates are based on the assumption that rose stars that were never seen again died during the course of the study. Other possibilities include emigration from Auke Bay or that they remained in deep water outside the SCUBA observation range. Although hundreds of rose stars were examined in and around Auke Bay during 1980 to 1997, no marked individual was ever found outside the study area, even in adjacent locations where the species is common, suggesting that survivorship estimates were unaffected by emigration to areas outside Auke Bay. Migration to deeper water remains a possibility and, if prevalent, would suggest that our survivorship estimates are an underestimate.

Population size

The number of *Crossaster papposus* sighted in each year was remarkably constant throughout the study period, averaging $185.2 (\pm 55.1$ SD) stars per year, with a maximum population size of 263 (natural log values shown in Fig. 5a). When these sightings were normalized to the number of dive-days in each year, the numbers remained relatively constant (Fig. 5a). Population size based only on sightings in any one year are almost certainly an underestimate of the total population, because *C. papposus* will migrate below SCUBA range. Thus, our second estimate of population size included an individual as present in any year if it was ever sighted in any subsequent year. These estimates of population size are uniformly higher than those in Fig. 5a, averaging $237.1 (\pm 73.8$ SD) stars per year, with a maximum population size of 338 (Fig. 5b). It is important to note, however, that total population estimates in the early and late years shown in Fig. 5b are underestimates due to proportionally less of the total population being marked at the beginning of the study, while in the later years of the study there were fewer subsequent years for resighting.

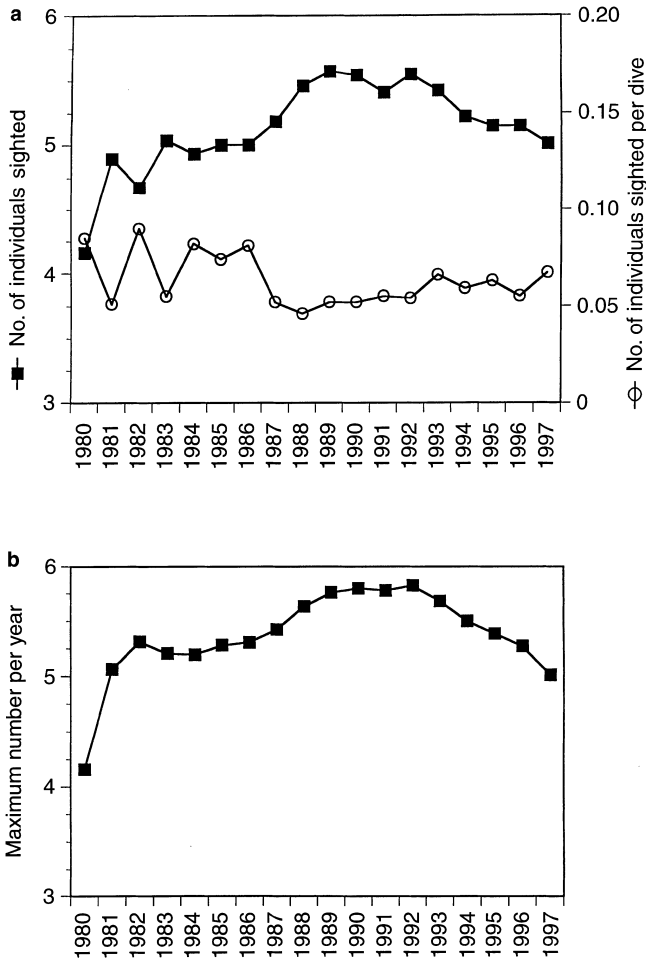


Fig. 5 *Crossaster papposus*. Natural log of population size. **a** Numbers of individuals sighted in each year and number of individuals sighted per dive; **b** estimated maximum numbers of individuals in population in each year (including any individuals seen in subsequent years)

Recruitment and immigration

The number of unmarked individuals that appeared in the population each year was 52.2 (± 23.8 SD), of which an average of 53.6% were ≤ 100 mm in diameter (Fig. 6). Throughout the study, the variability of the immigration rate of rose stars ≤ 100 mm was greater than that of individuals > 100 mm (a coefficient of variation of 76.4 vs 49.1). The number of stars ≤ 100 mm peaked in 1988 at 76, perhaps reflecting an earlier recruitment event. On average, stars ≤ 100 mm comprised 14.9% of the population ($SD = 8.6\%$). Unmarked individuals immigrated in all months of the year, resulting in no obvious pattern of seasonality to immigration, even when individuals ≤ 100 mm were grouped separately (Fig. 7).

Feeding habits

Rose stars in Auke Bay fed primarily on the reddish scallop (*Chlamys rubida*), which made up 80.5% of all

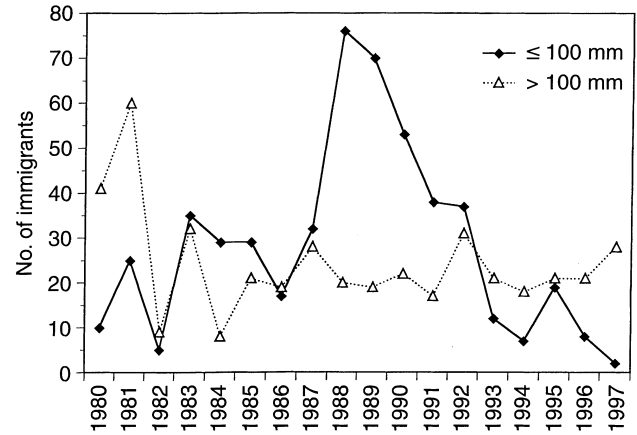


Fig. 6 *Crossaster papposus*. Number of immigrants (unmarked individuals) to population each year, divided into individuals ≤ 100 mm and > 100 mm in diameter

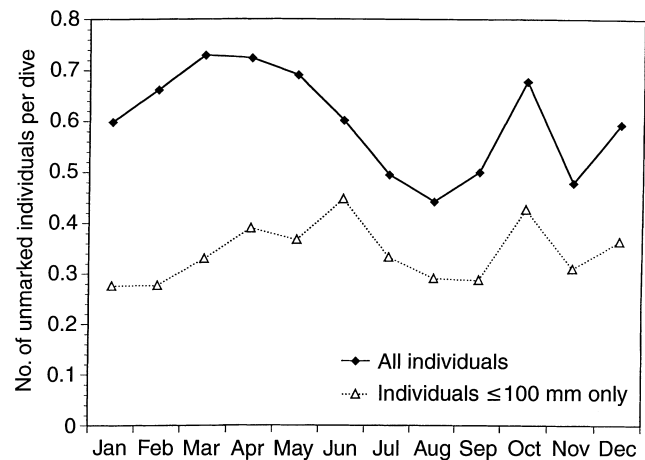


Fig. 7 *Crossaster papposus*. Number of immigrants (unmarked individuals) sighted each month (data pooled for all years). Pattern for all individuals is shown, and (separately) pattern for individuals ≤ 100 mm in diameter

food items (Table 1). Stars fed occasionally on other molluscs (6.0% of their diet) and infrequently on echinoderms (3.5% of their diet). With rare exceptions, rose stars avoided dead or injured prey; they were infrequently found feeding on fish remains or crab molts (1.9% of their diet). From 369 feeding observations in all months of the year, it was clear that there was no slack, nonfeeding period. Additionally, *C. rubida* was the principal prey item in all months of the year, ranging from 68.4 to 89.4% of the rose star diet in any given month.

Discussion

The *Crossaster papposus* population that utilizes our study site in Auke Bay is characterized by high survivorship and longevity and a relatively constant population size (Fig. 5). Relatively high survivorship was

Table 1 *Crossaster papposus*. Feeding habits in Auke Bay, Alaska, during all months of 1980 to 1996 ($n = 369$)

Prey	Frequency	%
Molluscs		
<i>Chlamys rubida</i>	297	80.5
<i>Clinocardium nuttali</i>	1	0.3
<i>Mytilus edulis</i>	5	1.4
<i>Mya truncata</i>	2	0.5
<i>Buccinum plectrum</i>	1	0.3
Limpets (unidentified)	3	0.8
<i>Placiphorella</i>	2	0.5
<i>Crepidula</i> spp.	1	0.3
<i>Dendronotus rufus</i>	1	0.3
<i>Onchidoris bilamellata</i>	1	0.3
Bivalves (unidentified)	4	1.1
Chiton (unidentified)	1	0.3
(Total molluscs)	(319)	(86.6)
Brachiopods		
<i>Terebratalia</i> spp.	1	0.3
Echinoderms		
<i>Strongylocentrotus droebachiensis</i>	6	1.6
<i>Leptasterias</i> spp.	4	1.1
<i>Evasterias</i> spp.	1	0.3
Brittle star (unidentified)	1	0.3
Asteroid star (unidentified)	1	0.3
(Total echinoderms)	(13)	(3.6)
Coelenterates		
<i>Ptilosarcus gurneyi</i>	2	0.5
<i>Aurelia aurita</i>	1	0.3
(Total coelenterates)	(3)	(0.8)
Crustaceans		
<i>Balanus</i> spp.	1	0.3
<i>Paralithodes</i> molt remains	3	0.8
(Total crustaceans)	(4)	(1.1)
Fishes		
<i>Clupea pallasii</i> remains	2	0.5
<i>Myoxocephalus</i> spp.	1	0.3
Cottidae (unidentified)	1	0.3
(Total fishes)	(4)	(1.1)
Unidentified matter	25	6.8

probably due to a lack of major predators on large individuals. Only one predator, the sun star *Solaster dawsoni*, was occasionally seen taking a large rose star. Small *C. papposus* (≤ 50 mm) often have more cryptic habits and may be more vulnerable to predation.

Although mortality rates of small individuals (< 50 mm) are unknown, *Crossaster papposus* has a relatively high longevity. Two of the 64 individuals marked in 1980 persisted through 1997, and growth and survivorship data indicate that many individuals in the population can live for many years. Interestingly, one individual was near 180 mm at the beginning of the study and grew relatively little over 16 yr, suggesting that some rose stars can live well in excess of the 17 yr that this study encompassed. Indeed, the size and age relationships predicted by the regression of size and growth indicated that individuals as small as 160 mm may be ≥ 20 yr of age (Fig. 4). Additionally, survivorship estimates indicate that some individuals live beyond 20 yr of age. Unfortunately, we do not know the survivorship

of larval and juvenile stages, although a study of another sea star (*Pisaster ochraceus*) suggests that 99% of all individuals die within their first year of life (Sewell and Watson 1993; Gosselin and Qian 1997).

Rose stars grow relatively slowly to a maximum size and take years to regenerate lost arms, with larger individuals showing the slowest rates of growth (Fig. 2). A decrease in growth with size is a feature common to other invertebrates, especially molluscs (Frank 1969; Spight 1981; Parry 1982) and fishes, and is the basis for widely-used growth models such as the von Bertalanffy growth model (Cushing 1981). Although many invertebrates have indeterminate growth, these often grow to some maximum size, with negligible growth thereafter ("plastic asymptotic growth": Sebens 1987). The asymptotic approach to a maximum size that a sea star attains may also be a function of the resource levels at a site and the density of the sea star population. For example, Paine (1976) showed that the mean size of the sea star *Pisaster ochraceus* was inversely related to population density over a variety of sites on the outer coast of Washington state. Individuals transplanted from a high- to a low-density site were capable of increasing greatly in size relative to controls that were transplanted back to the same high-density site, suggesting that the size of sea stars in a given area is density-dependent.

The population size of *Crossaster papposus* at our study site in Auke Bay varied remarkably little during the 17 yr of the study (Fig. 5). Constancy in population size is not always a feature of sea star populations; indeed, cyclic fluctuations (*Asterias forbesi*: Burkenroad 1946) and local outbreaks (*Acanthaster planci*: Birkeland 1982) have been noted in other sea star species. The greatest difference in the population density estimated by either simple counts or based upon subsequent re-sightings (Fig. 5a and b, respectively) occurred in 1991, when 100 more individuals (or 31% of the population) were counted as present than were actually seen. However, the peak in population size coincides in both a and b of Fig. 5, indicating that the maximum population size at our study site in Auke Bay was 338 individuals. On average, 22.6% of the total population was uncounted in any given year, and presumably had migrated to depths just below SCUBA limits. Despite the potential for movement between shallow and deep water (> 50 m), bottom-trawl samples suggest that the *C. papposus* population is concentrated in shallow areas. One hundred trawl samples during all seasons and several years showed only a single occurrence of *C. papposus* in 50 to 100 m depths in Auke Bay (Carlson et al. 1982).

Although the number of ≤ 100 mm immigrants varied over an order of magnitude (Fig. 6), it is not yet clear whether this reflects episodic recruitment events, such as those described for other echinoderm species (Ebert et al. 1994; Loosanoff 1964) and other benthic invertebrates (Coe 1956). The variability documented in the number of ≤ 100 mm immigrants was not paralleled by any similar fluctuation in the entire population size, which remained relatively constant (Fig. 5a). Although seasonal migra-

tory patterns associated with the formation of breeding aggregations have been recorded for a number of invertebrates, including snails (e.g. *Thais lamellosa*: Spight 1974), *Crossaster papposus* showed no seasonal pattern in the appearance of unmarked individuals (Fig. 7). Additionally, during 17 yr of study, few instances of breeding activity were observed, and the reproductive biology of *C. papposus* remains known largely from laboratory individuals (Strathmann 1987). Although, based on our failure to observe marked individuals outside the study area, the benthic *C. papposus* population we followed in Auke Bay is relatively discrete, little is known about the distance to which its larvae are capable of dispersing.

Movement patterns of *Crossaster papposus* may be influenced more by feeding behavior than by breeding requirements. Because their principal prey item, the reddish scallop, is rarely seen deeper than 30 m in Auke Bay, it may influence local rose star depth-distribution and movements. Despite the clear specialization of *C. papposus* on the reddish scallop in Auke Bay, the feeding behavior of *C. papposus* varies greatly over its geographic range (Sloan 1980). In Puget Sound, Mauzey et al. (1968) observed ($n = 131$) that rose stars on sand substrate fed mostly on sea pens, *Ptilosarcus gurneyi* (50%), opisthobranchs (34%), and occasional anemones, results also found by Birkeland (1974). Mauzey et al. (1968) observed rose stars on cobble substrate feeding only three times: once each on a nudibranch (*Dirona albolineata*), an ascidian (*Ascidia paratropa*), and a scallop (*Chlamys* spp.). Most of the feeding observations of rose stars in Auke Bay were on hard substrate – rock ledges, cobble, boulders, and sometimes on adjacent broken shell/sand – all locations where reddish scallops were common or abundant, as were other potential prey such as the small asteroids *Evasterias troschelii* and *Leptasterias* spp. Also seasonally common at the Auke Bay study site were nudibranchs of the genera *Cadlina*, *Coryphella*, *Triopha* and *Dendronotus*, but all were absent or rare in rose star diets.

Although the causes for relative constancy in *Crossaster papposus* numbers cannot be determined from this study, there are several plausible explanations. For example, the relative stability of the population may be related to constancy in the abundance of its principal prey, the reddish scallop, or to *C. papposus*' ability as a generalist consumer across its geographic range (Mauzey et al. 1968; present study), an ability presumed to provide stability in populations of the marine gastropod *Conus pennaceus* (Perron 1983). An additional hypothesis is that larval development-mode influences population stability, with the lecithotrophic larvae that characterize *Crossaster papposus* contributing a constant influx of new individuals (sensu Thorson 1950). However, despite the association between species with planktotrophic larvae and the incidence of large population fluctuations (such as the outbreaks observed for the crown-of-thorns sea star *Acanthaster planci*: Birkeland 1982), there remains little evidence that a lecithotrophic development mode dampens population fluctuations (Levin and Huggett 1990).

Although much of our understanding of the dynamics of marine invertebrate populations and the process important to their persistence along rocky shores has come from shorter-lived species, there are also a number of species which show survivorship and longevity patterns similar to those of *Crossaster papposus*. Mussels, a dominant member of nearshore rocky shores, can also be long-lived (20 yr based on Frank 1969), although those in areas of intense disturbance are likely to be shorter-lived (Paine and Levin 1981). The ascidian species *Pyura tessellata* lives in excess of 11 yr on the Swedish west coast (Svane 1983). Gastropods, including *Tegula funebris* in the northeast Pacific, have survivorship rates similar to *C. papposus*, and size and age relationships indicate that individuals may live for >20 yr (Paine 1969). Similarly, the keystone sea star species *Pisaster ochraceus* may also be relatively long-lived (Paine 1966, 1976). When marine invertebrates capable of asexual reproduction are considered (anemones, coral), marine invertebrate lifespans may reach multiple decades (Sebens 1983; Connell et al. 1997).

Shorter-lived invertebrates have provided us with a wealth of information on the dynamics of populations and the interactions among species (e.g. Connell 1961; Sutherland 1974; Levin et al. 1987), but we know less about the dynamics of long-lived species. Recent attempts to synthesize demographic information among multiple taxa demonstrate that several features of long-lived species may make their dynamics distinct from those of short-lived species, including the high sensitivity of population growth to small changes in adult survivorship and its relatively low sensitivity to fecundity (Silvertown et al. 1993; Benton and Grant 1996). Despite the generalization that fecundity contributes less to population growth as lifespan increases, some relatively long-lived marine species are still capable of showing rapid population increases (or outbreaks) during episodic recruitment events (e.g. crown-of-thorns sea star: Birkeland 1982). Long-term studies (such as the present one) on the demography of dominant members of marine communities are the basis for understanding how long-lived species recover from anthropogenic disturbances (e.g. pollution), respond to alterations in the abundance of other species (e.g. harvesting), and adjust to large-scale environmental change.

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