

Rates of fission, somatic growth and gonadal development of a fissiparous sea star, *Allostichaster insignis*, in New Zealand

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Abstract Seasonal changes in population structure and incidence of fission were measured in intertidal and subtidal populations of *Allostichaster insignis*, a fissiparous sea star. Population size structure was stable over the course of the 1-year study. Sea stars in the subtidal zone attained greater maximum size (mean arm length, $R = 35$ mm) than those in the intertidal population (20 mm). Fission rates were greatest among small individuals ($R < 20$ mm). The frequency of fission ranged from 5 to 32% with peaks in early austral summer in the intertidal zone, and in autumn and winter in the subtidal zone. Sexual reproduction occurred in early spring in sea stars larger than 12 mm. The populations were heavily biased toward males. In the laboratory, *A. insignis* of three size classes (small, $R = 9$ –13 mm; medium, 19–21 mm; and large, 29–31 mm) were fed mussels ad libitum or starved (not fed macroscopic food) for ~ 1 year in a 3×2 factorial experiment. Small and medium-sized sea stars divided throughout the experiment and the ramets of most individuals regenerated sufficiently to divide again after 6–9 months. Unfed sea stars did not undergo fission (with one exception), had a higher mortality rate, and did not grow. Small, fed sea stars grew significantly faster than medium-sized or large individuals. At the end of the experiment, the pyloric caeca index (a

measure of nutritional condition) was greater in fed than in unfed animals. Gonads (only testes were observed) developed in medium-sized and large, fed sea stars. Our field and laboratory results indicate that asexual reproduction in *A. insignis* predominantly occurs in small, well-nourished individuals. Ramets grow gradually through repeated fission and regeneration to a size (mean length of regenerating arms, $R_r \sim 20$ mm) at which they begin to switch to sexual reproduction as the dominant reproductive mode.

Introduction

Asexual reproduction occurs in a variety of marine invertebrate taxa by mechanisms such as fission, budding, and fragmentation (Giese and Pearse 1974; Hughes 1989; Mladenov 1996). In almost all cases, asexual species are heterogonic: able to reproduce by both sexual and asexual means. However, the biotic and abiotic factors that regulate the expression and relative proportion of asexual and sexual phenotypes within populations of such species, and the factors triggering asexual reproduction, are poorly understood. In sea anemones, asexual reproduction has been associated with physiological stress, small body size and poor nutrition (Chia 1976; Johnson and Shick 1977; Francis 1988), although there have been few experimental tests of these factors. Studies of the effects of food availability have yielded contrasting results in different species of anemones: fission rate has been shown to increase with starvation (Smith and Lenhoff 1976; Sebens 1979, 1980) or increased feeding (Minasian 1976; Johnson and Shick 1977; Bucklin 1987; Lin et al. 1992; Hand and Uhlinger 1995).

Asexual reproduction in echinoderms occurs by fission of the adult body within the classes Holothuroidea, Ophiuroidea and Asteroidea. Within the Asteroidea, at least 21

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species are fissiparous or able to reproduce asexually by splitting in half and regenerating the missing part of the disk and arms of each ramet (Emson and Wilkie 1980; Mladenov and Burke 1994; Mladenov 1996). Intraspecific variation in the relative importance of asexual and sexual reproduction has been documented in sea stars at both geographic and local (between-habitat) scales. Latitudinal gradients in the incidence of fissiparity in some species [e.g., *Asterina burtoni* (Achituv 1969; James and Pearse 1969), *Nepanthia belcheri* (Kenny 1969)] suggest that harsher, seasonally varying temperate environments favour asexual reproduction, whereas sexual reproduction is the dominant mode in the more benign tropics. Other studies have documented variation in the incidence of asexual and sexual reproduction between subtidal and intertidal populations of sea stars within the same geographic locale. For example, subtidal populations of *Allostichaster polyplax* and *Coscinasterias muricata* generally have a larger body size, lower incidence of fission, and larger gonads than intertidal populations subjected to greater stress and poorer feeding conditions (Emson 1978; Crump and Barker 1985). In some populations of *C. muricata* in southern New Zealand fiords, asexual reproduction by fission does not appear to occur at all (Sköld et al. 2002). From field observations and the results of a laboratory feeding experiment Sköld et al. (2002) suggested that the occurrence of apparently fewer fissiparous individuals in habitats where food is abundant is correlated to food supply, i.e., where food is abundant fission is not as common.

Fission in sea stars is generally a seasonal phenomenon, suggesting that fluctuating environmental factors such as sea water temperature and photoperiod modulate the asexual reproductive cycle (Mladenov 1996). Physical disturbance and physiological stress (e.g., desiccation, hyperthermia, or hypoxia) may trigger fission in highly variable environments, such as the intertidal zone (Emson and Wilkie 1980; Alves et al. 2002). The frequency of fission also may be related to body size in some species. For example, Crump and Barker (1985) found that fission was more frequent in small individuals of *Coscinasterias muricata*. However, Ottesen and Lucas (1982) found no relationship between fission frequency and body size in *Nepanthia belcheri*.

Allostichaster insignis (Farquhar) is a fissiparous sea star (family Asteriidae) that ranges from the intertidal zone to depths of ~300 m in the South Island and southern parts of the North Island of New Zealand (M. F. Barker, unpublished data). Large specimens attain mean arm lengths up to 75 mm, although populations generally are dominated by smaller individuals (mean arm length <20 mm) (Barker et al. 1992). Most individuals have six arms and fission normally divides the body evenly into two halves, each with three arms. In this study, we document seasonal changes in

size structure and frequency of fission in intertidal and subtidal populations of adult *A. insignis* in Otago Harbour, South Island, New Zealand. Also, we examine the hypothesis that fission and nutrition are linked by examining the effects of nutritional stress and body size on rates of fission, somatic and gonadal growth, and arm regeneration in a laboratory experiment. Our findings shed light on proximal factors that may regulate asexual and sexual reproduction in *A. insignis*, and on the adaptive significance of these alternative reproductive modes.

Materials and methods

Study site and field measurements

We sampled populations of *A. insignis* at two adjacent sites at Aquarium Point in Otago Harbour (170°38.5'E: 45°50'S): (1) a sandy intertidal shore with cobbles and small boulders, and (2) a coarse sand and shell rubble bottom ~50 m offshore of the intertidal site at 2–5 m depth. Sea stars at the subtidal site were found mainly on dense mats of filamentous red alga (*Lenormandia chauvini*) that covered much of the bottom. At each site, we collected *A. insignis* in 15 randomly placed 1-m² quadrats along a fixed belt transect running alongshore (3 × 25 m at the intertidal site, 2 × 25 m at the subtidal site). We carefully searched each quadrat for cryptic individuals on undersides of rocks or within algal mats. Arm lengths of each sea star were measured (1-mm accuracy) along the oral side of the arm from mouth to arm tip for all arms. Because fission in *A. insignis* typically produces two 3-armed ramets that subsequently each regenerate a new set of three arms, we differentiated between measurements of these regenerating arms (with mean R_r) and the original (for that ramet), longer arms (with mean R_o). Mean overall arm length (R) was calculated as the average of all arms. Newly divided sea stars were assigned $R_r = 0$ mm for the three potentially regenerating arms. After measurement in the laboratory, sampled sea stars were held in running seawater and returned within 24 h to their respective collection site. Sampling at both sites was conducted at 2–3-month intervals from October 1989 to October 1990.

To determine the reproductive condition of *A. insignis*, we collected specimens ranging in R_o from 12 to 40 mm on each of three dates at the subtidal site (October 1989, $n = 5$; September 1990, $n = 15$; October 1990, $n = 8$; February 1991, $n = 10$), and once at the intertidal site (September 1990, $n = 9$). The sea stars were dissected and the gonads and pyloric caecae (in February 1991 only) were removed and weighed (0.001-g accuracy). Gonad and pyloric caecae indices were calculated as the respective organ wet weight expressed as a percentage of the eviscerated wet body

weight. The sex of each dissected specimen was determined by microscopic examination of a gonadal smear.

Laboratory experiment

A. insignis for the laboratory experiment were collected on 30 January 1989 at the subtidal site. Only 6-armed individuals with arm lengths differing by <2 mm (i.e., individuals in which fission had not recently occurred) were used. Thirty-six sea stars were sorted into three size classes based on R : small (9–13 mm), medium (19–21 mm), and large (29–31 mm). These classes were selected to represent sea stars that were immature, just reaching reproductive maturity, and mature, respectively, and to span the size range over which fission occurs naturally (see “Results”). Each size class was further divided into a fed and an unfed group. The fed group was offered small (5–25 mm shell length) live mussels (*Xenostrobus pulex*, collected from a nearby rocky shore) ad libitum throughout the experiment. Mussel size varied in proportion to sea star size among the three experimental size classes. The unfed group had no macroscopic food. Six replicate specimens were randomly allocated to each combination of size class and feeding regime in a 3×2 factorial design. They were individually placed in coded 300 ml plastic jars with 1-mm mesh panels on the tops and sides to allow water exchange, and each was provided with a small rounded pebble (collected from the nearby intertidal zone) for shelter and attachment. The jars were immersed in six flow-through seawater tanks (143 cm length \times 73 cm width \times 24 cm depth) running along one wall of the laboratory. Each tank received six jars, one of each treatment combination and each jar received seawater at flow rates of 0.3–0.5 l min^{-1} . Light was provided on a natural cycle from nearby windows and fluorescent ceiling lights. Seawater was supplied at ambient temperature, ranging from 7 to 15.5°C during the experiment.

Experimental individuals were checked at weekly intervals. Mussels that had been consumed were replaced and the inside walls of jars were wiped to limit biofouling. When a sea star divided, the ramets were individually placed in two recoded jars and returned to the same seawater tank. Individuals were measured at about monthly intervals. Care was taken to limit disturbance when removing them for measurement, since forcible detachment may cause autotomy of arms, especially in starved animals. Dead sea stars were immediately removed from the experiment. The experiment was terminated on 22 January 1990 after \sim 1 year. All experimental individuals were measured and the pyloric caecae and gonads (where present) were removed and wet weighed (0.001-mg accuracy). Gonad and pyloric caecae indices were calculated as described above.

Results

Field populations

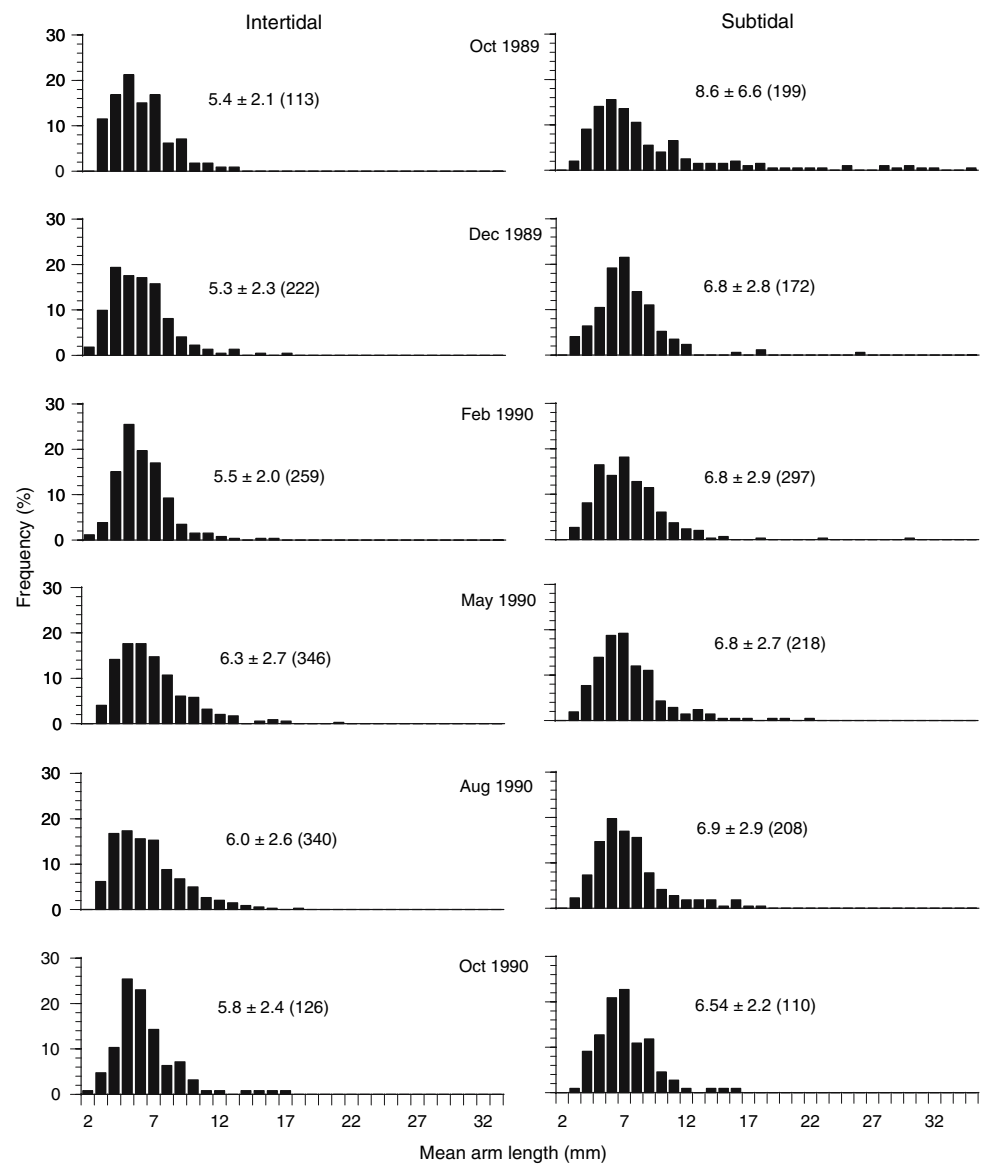
Size frequency distributions (mean arm length, R) of *A. insignis* in both the intertidal and the subtidal population were relatively stable over our 1-year study (Fig. 1). Size distributions were positively skewed with small sea stars (5–7 mm) representing the most abundant size classes in both populations. R was consistently larger in the subtidal population (up to 35 mm), where 3% of sea stars (all samples combined) exceeded the maximum size recorded in the intertidal population (20 mm). A few recently settled sea stars ($R < 3$ mm) were collected in the intertidal zone in December 1989 and in February and October 1990.

The temporal pattern of fission rate, measured as the percentage of recently divided *A. insignis* (defined by the ratio of regenerating-to-original mean arm lengths: $R_t/R_o < 0.05$), differed between intertidal and subtidal populations (Fig. 2). In the intertidal population, the frequency of fission was greatest in austral spring and early summer 1989 (up to 32%), fell sharply by late summer (5%), and remained low through autumn and winter before increasing again in spring 1990. In the subtidal population the frequency of fission was low in summer (6–12%) and increased in autumn and winter to higher levels (20–24%) than those observed in the intertidal population. Contingency table analysis using a log-linear model (G test) showed a significant 3-way interaction of fission frequency, sampling date and habitat ($G = 66.97$, $df = 5$, $P < 0.001$). Within each habitat there was a significant 2-way interaction of fission frequency and sampling date (subtidal: $G = 22.7$, $df = 5$, $P < 0.001$; intertidal: $G = 80.4$, $df = 5$, $P < 0.001$).

The frequency of fission among different sized sea stars was compared by plotting the coefficient of variation of arm length against the mean (R), and shows a non-linear negative relationship for both the intertidal and the subtidal population (Fig. 3). High variability in arm length among small sea stars ($R < 10$ mm) indicates they are regenerating arms after fission; low variability among larger individuals ($R > 20$ mm) indicates they have not undergone fission for some time and their arms have completely regenerated.

The sex ratio of *A. insignis* was highly skewed towards males: only two females (5%) were recorded out of a total of 38 specimens with macroscopic gonads, one in each population in September 1990. Nine out of the 47 specimens that we sampled did not have macroscopic gonads; in these R ranged from 13 to 24 mm. The gonad index of males of *A. insignis* was significantly greater in the subtidal than intertidal population in September 1990 (t test, assuming unequal variance, $t = 2.18$, $df = 12$, $P = 0.018$) (Fig. 4).

Fig. 1 *Allostichaster insignis*. Size frequency distributions of intertidal and subtidal populations over 1 year. Data are mean \pm SD, sample size is in parentheses



By October 1990, some individuals in the subtidal population had spawned, as indicated by a decrease in gonad index to a level comparable to that observed in October 1989. In February 1991, all males sampled from the subtidal population were spent, although some active sperm were observed in gonadal smears. The highest gonad index (27.3) was recorded for the single female sampled in the subtidal population in September 1990; this specimen was fully ripe with mature eggs. The female sampled in the intertidal population at that time had a much lower gonad index (1.70), but also had mature eggs. There was no relationship (adjusted $R^2 = 0.020$) between the gonad index of male *A. insignis* and mean arm length (for R ranging from 12 to 25 mm) in the subtidal population in September 1990 (when we had the greatest sample size). Gonads were not observed in regenerating arms.

Laboratory experiment

Fission in *A. insignis* is similar to that described for *A. polyplax* by Emson and Wilkie (1980). The two opposing sets of three arms pull against each other and a fission plane gradually forms across the disk. Fission in our experiment took several hours to complete. The wounds healed within 1–2 weeks and we observed new arm buds (0.5–1.0 mm in length) within 5–8 weeks. Twin buds appeared first with a third emerging between them 2–3 weeks later.

Six of the 36 initial animals died during the experiment without dividing (Table 1): four (three small, one large) from the unfed treatment and two (both small) from the fed treatment. Since neither of the two sea stars in the fed treatment ate mussels during the experiment, all of the dead animals had not eaten. There was no apparent relationship

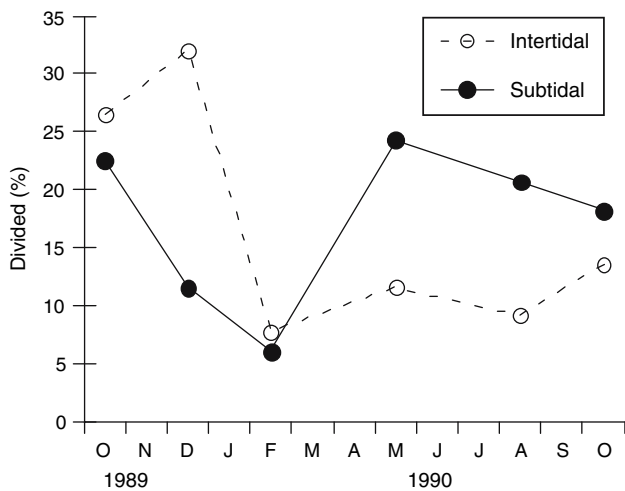


Fig. 2 *Allostichaster insignis*. Temporal changes in the percentage of recently divided sea stars (ratio of regenerating to original long arms < 0.05) in intertidal and subtidal populations

between treatment and time of death: the first mortality was a small, fed sea star within 3 weeks of the start of the experiment, while the last two mortalities were small and large, unfed sea stars after ~ 10 months.

There was a marked effect of feeding regime and body size on the incidence of fission in *A. insignis* (Table 1). Only 1 small individual of 14 surviving in the unfed treatment underwent fission. In contrast, fission occurred in 9 of 16 individuals in the fed treatment. Both ramets of 4 of these (2 small, 1 medium, 1 large) subsequently divided as well, as did 1 of 2 ramets of a medium-sized individual. In the fed treatment, small (3 out of 4) and medium-size (5 out of 6) individuals of *A. insignis* divided more frequently than large ones (1 out of 5) ($\chi^2 = 6.18$, $df = 2$, $P = 0.01$).

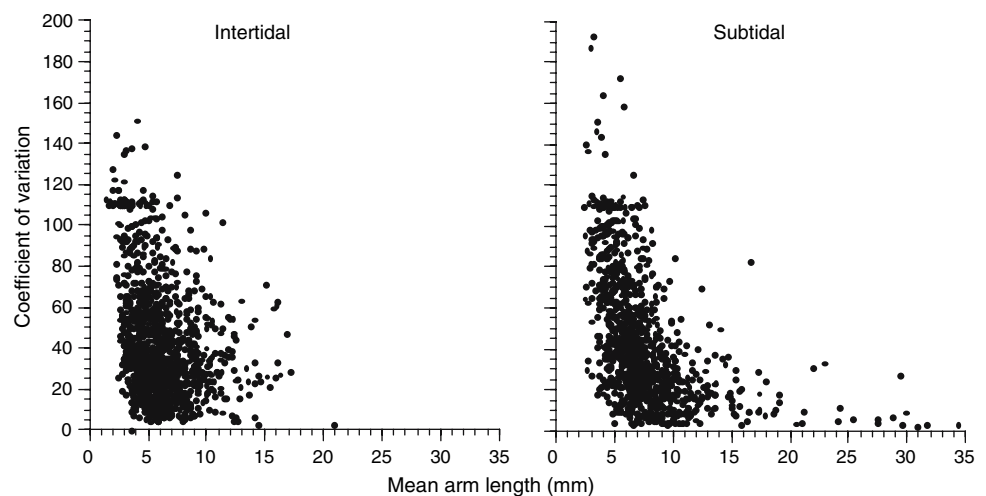
Changes in R_0 and R_r of nine specimens of *A. insignis* that divided are shown in Fig. 5. (One of the five medium-sized sea stars that divided subsequently lost one of the three long arms after dividing and this is noted on this

figure). A comparison of the linear regression slopes of arm length against measurement day (from the start of the experiment) shows that regenerating arms grew faster than original arms for both small (paired-samples t -test: $t = 7.13$, $df = 5$, $P < 0.001$) and medium-sized ($t = -11.02$, $df = 7$, $P = < 0.001$) sea stars in the fed treatment. All ramets within an initial size treatment were considered independent replicates because they were reared in separate jars. In the only unfed individual that divided, the original arms decreased in length and there was little growth of regenerating arms beyond the arm bud stage.

Fission in the ramets produced during the experiment occurred once their regenerating arms had grown substantially, but before these arms had reached the length of the original arms (e.g., Medium-Fed #4, Fig. 5). In four of the five individuals that divided a second time, fission occurred late in the experiment (217–280 days) and growth of the second set of regenerating arms is not shown in Fig. 5. There was no significant difference between small and medium sea stars in the time (from the start of the experiment) to either the first ($t = 1.79$, $df = 7$, $P = 0.133$) or second division ($t = 0.98$, $df = 6$, $P = 0.371$) (Fig. 6). The interval between two successive divisions ranged from 165 to 280 days. Fission was relatively synchronous between ramets of the same individual (genet). For example, ramets of one individual (Small-Fed #2, Fig. 5) divided on the same day, 8 months after they were formed from the division of the original parent; ramets of another individual (Medium-Fed #4, Fig. 5) divided within 3 weeks of one another, 7 months after their formation.

All fed individuals grew in total arm length (all arms of all ramets summed) and growth curves followed the same general pattern among the three size classes (Fig. 7), except for one (Medium-Fed #4, Fig. 5) that divided twice and grew substantially more than the other medium-sized sea stars, and another that autotomised an arm early in the experiment and did not feed or grow thereafter. Total

Fig. 3 *Allostichaster insignis*. Coefficient of variation of arm length versus mean arm length for all seastars sampled from subtidal and intertidal populations



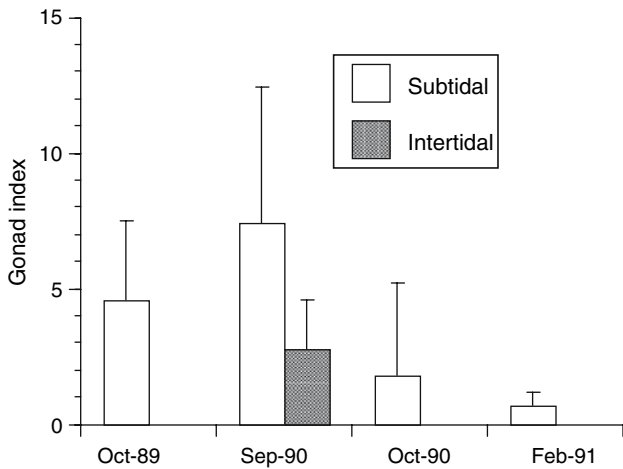


Fig. 4 *Allostichaster insignis*. Male gonad index (mean ± SD) of subtidal ($N = 5-10$) and intertidal ($N = 7$, September 1990 only) populations

Table 1 *Allostichaster insignis*. Divided and undivided individuals, and those that died, among three size classes and two diet treatments in the laboratory experiment

	Small		Medium		Large	
	Fed	Unfed	Fed	Unfed	Fed	Unfed
Undivided	1	2	1	6	5	5
Divided	3	1	5	0	1	0
Died	2	3	0	0	0	1

growth rate, expressed as the percentage change in total arm length during the experiment (Fig. 8) differed significantly among size classes in the fed treatment (ANOVA, $F = 6.44$, $df = 2,13$, $P = 0.011$), with small sea stars growing significantly more than large ones (Student Newman Keuls test, $P < 0.05$). None of the unfed sea stars grew and all size classes had decreased in total arm length by 20–25% at the end of the experiment (Figs. 7, 8).

At the end of the experiment, the pyloric caeca index (Fig. 9) was markedly larger in fed than in unfed *A. insignis* for all size classes (pyloric caecae of small, unfed sea stars were too small to accurately measure). Pyloric caeca indices of fed sea stars were comparable to (Small: equal means; Medium: $t = -0.33$, $df = 7$, $P = 0.752$), or significantly greater than (Large: $t = -3.05$, $df = 6$, $P = 0.023$), indices of similar sized individuals from the field population (measured concurrently). None of the sea stars in the unfed treatment, nor any of the small fed sea stars, had developed gonads by the end of the experiment. Only one medium sea star had gonads; this individual had a higher gonad index (4.5) than any of the large animals. The gonad index of large, fed sea stars did not differ significantly from field-collected sea stars of similar size ($t = 1.06$, $df = 7$, $P = 0.326$). All sea stars in these comparisons were male.

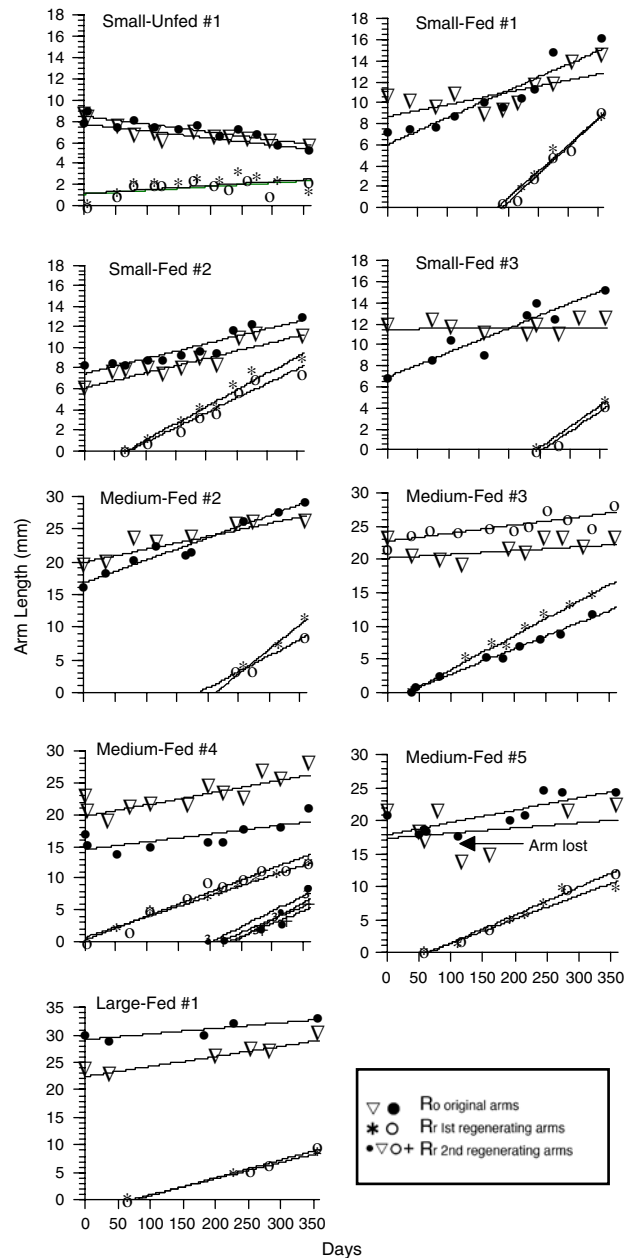


Fig. 5 *Allostichaster insignis*. Growth rates of original and regenerating arms of individuals that divided in the laboratory experiment. Lines are linear regressions fitted to the data: mean length (mm) of original (R_0) and regenerating (R_1) arms (two sets, the first from the first division and the second from regenerating seastars that divided again) against time (d) from the start of the experiment

Discussion

Size frequency distributions were relatively stable in both the intertidal and subtidal population of *A. insignis* over our 1-year study, and mean and maximum arm length of sea stars were greater in the subtidal population. Recently settled sea stars ($R < 3$ mm) were rare and found only in the

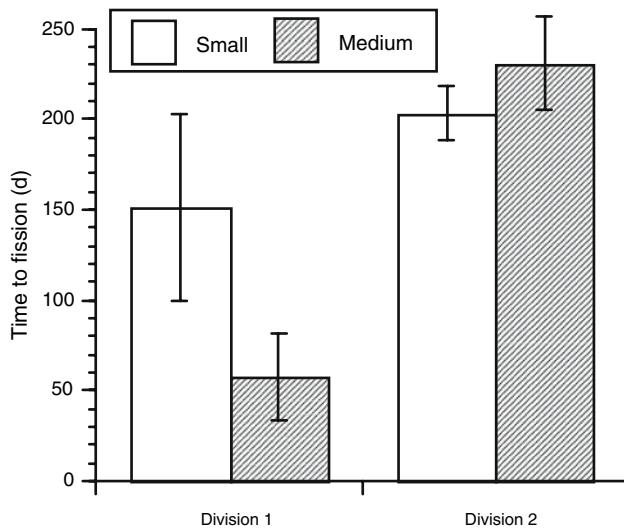


Fig. 6 *Allostichaster insignis*. Time from the start of the experiment (mean \pm SE) until the first and second divisions in small ($N = 4$) and medium-sized ($N = 4$ –5) individuals that divided in the laboratory experiment

intertidal zone, indicating that recruitment from sexual reproduction may be sporadic or low in these populations. The frequency of fission ranged from 5 to 32% with seasonal trends that differed between habitats: fission rate was highest in early summer in the intertidal zone, and in autumn and winter in the subtidal zone. Seasonality in rates of fission has been reported in other sea stars. Fission occurs in spring or summer in *Allostichaster capensis* (Rubilar et al. 2005), *Stephanasterias albula* (Mladenov et al. 1986), *Coscinasterias acutispina* (Yamazi 1950, Fujita 2001), and *C. tenuispina* in Bermuda (Crozier 1920), although Alves et al. (2002) found that fission in *C. tenuispina* was more common in winter in Brazil. Fission in *Nepanthia belcheri* also occurs in winter (Ottensen and Lucas, 1982).

Between-habitat differences in the temporal pattern of fission rate may reflect seasonal differences in food availability or foraging ability of sea stars. There was no apparent seasonality in fission rates during our experiment, but the results clearly show that starvation limits fission in this species. Only one small, unfed sea star (7% of survivors) underwent fission whereas nine (56%) divided in the fed treatment, and ramets of five of these nine divided as well. Similarly, Sköld et al. (2002) found that only fed individuals of *Coscinasterias muricata* divided in a laboratory experiment. Fujita (2001) also found that fed *C. acutispina* divided in the laboratory, although his experiment did not contain a starved treatment. Uthicke (1997) found that fission rates in a tropical sea cucumber *Holothuria atra* were higher in areas where sediments had a greater nutritional value. These results are inconsistent with previous

suggestions that nutritional stress may induce fission in asexually reproducing echinoderms (Emson and Wilkie 1980; Crump and Barker 1985).

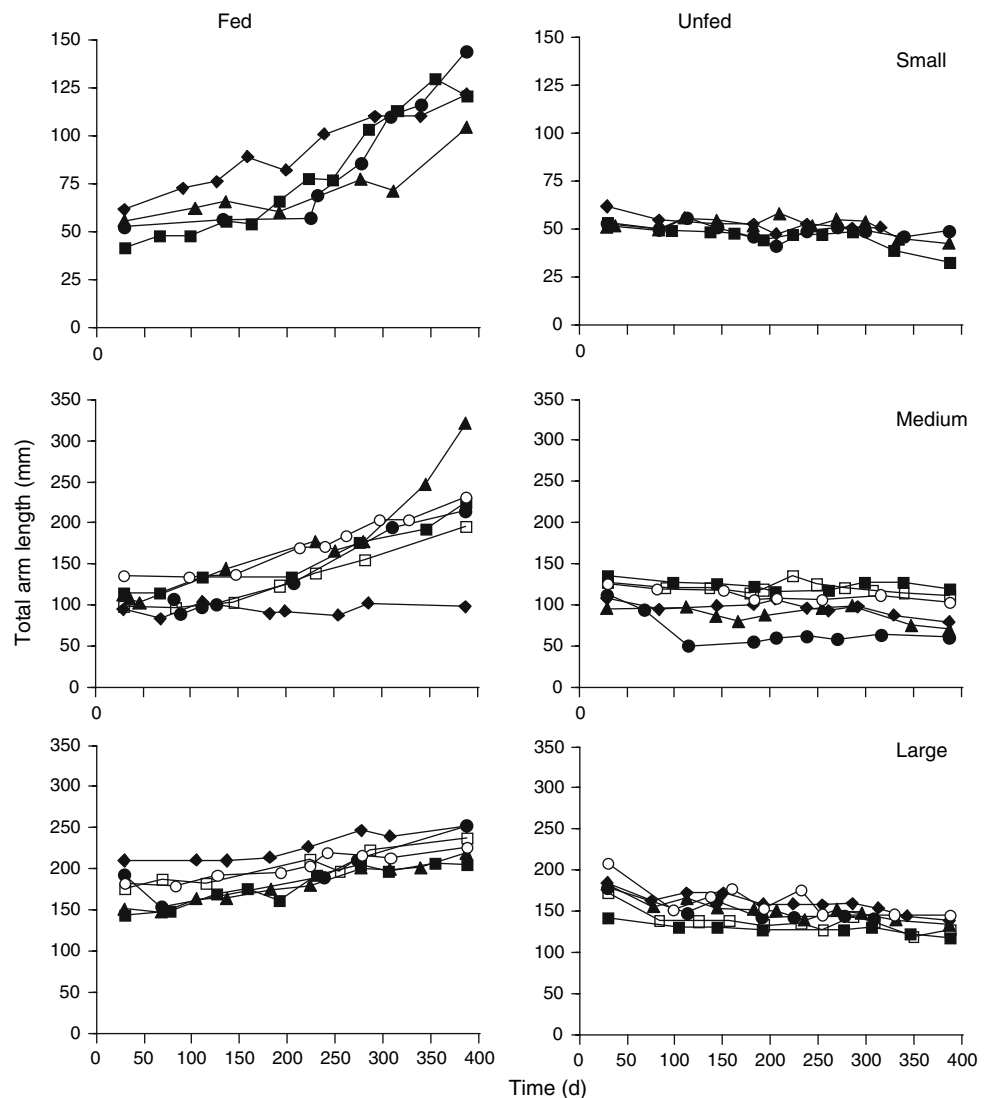
Fission and subsequent arm regeneration may pose an important nutritional cost to sea stars, such that it occurs only when adequate food is available. Autotomy and fission are similar phenomena with similar costs. Lawrence and Larrain (1994) showed that *Stichaster striatus* with recently autotomised arms have 40% less lipid and 85% less energy stored in the pyloric caeca compared to sea stars with intact arms, and Diaz-Guisado et al. (2006) found that autotomy was associated with decreased feeding and growth of this species. At the end of our experiment, the pyloric caeca index of *A. insignis* was minimal in unfed compared to the fed sea stars. Limited energy reserves may account for the negligible arm regeneration of ramets of the single unfed individual that divided. Regeneration of missing arms and repair of the digestive tract is a prerequisite for feeding and nutrient assimilation to support further growth.

A. insignis in the fed treatment regenerated new arms rapidly to the point where ramets divided 6–9 months after fission of the parent. This is faster than the fission rate of *Stephanasterias albula* in the Bay of Fundy, Canada, which divides once every 1–2 years (Mladenov et al. 1986), and *Asterina burtoni* on the Mediterranean coast of Israel, which divides about once per year (Achituv and Sher 1991). In laboratory studies, complete arm regeneration following autotomy took more than 12 months in *Asterias rubens* (Ramsay et al. 2001) and only ~25% regeneration was evident after 5 months in *Stichaster striatus* (Diaz-Guisado et al. 2006). Fission and arm regeneration rates that we observed for *A. insignis* in the fed treatment may be somewhat faster than those in nature, since experimental sea stars were fed a rich food source (mussels) ad libitum. The greater pyloric caeca of large, fed animals compared to field-collected animals suggests that experimental animals were better nourished. Our results are comparable to fission rates of laboratory-fed *Coscinasterias acutispina* measured by Fujita (2001), who found that four out of six individuals divided over a 6-month period, two of them twice.

In the paired ramets of *A. insignis* that divided, fission was relatively synchronous. Those of one individual divided on the same day; fission in other paired ramets occurred days or weeks apart. Fission apparently occurs once the regenerating arms attain a critical minimum length of at least 80% of the original arm length, and the apparent synchrony of division among ramets reflects similar growth rates of individuals of similar initial size under similar experimental conditions.

Repeated fission of small *A. insignis* in our fed treatment begs the question: How is large size attained in a good nutritional environment? It seems likely that even though small sea stars may divide once or twice a year, the ramets

Fig. 7 *Allostichaster insignis*. Increase in total arm length (sum of all arms of all ramets) of fed and unfed animals in small, medium, and large size classes in the laboratory experiment. Each symbol represents a different individual



must gradually increase in size as the larger (older) arms slowly continue to grow. When growth is measured as percentage change in total arm length, small *A. insignis* grew significantly faster than large sea stars in the fed treatments. Faster growth in small (immature) sea stars likely reflects a greater allocation of resources to somatic growth, whereas larger ones allocate resources to both growth and sexual reproduction.

Greater rates of fission in small and medium-sized *A. insignis*, relative to large individuals in the fed treatment, is consistent with the dominance of small fissiparous size classes in intertidal field populations. More frequent fission in smaller individuals has been reported for other sea stars (Yamazi 1950; Kenny 1969; Emson and Wilkie 1980; Crump and Barker 1985; Mladenov et al. 1986) and ophiuroids (Mladenov and Emson 1984; Mladenov and Burke 1994). Large individuals of *A. insignis* ($R = 30\text{--}35$ mm) occasionally were found in the subtidal habitat. These typically had six evenly-sized arms and rarely showed evidence

of fission, indicating that fission either ceases or occurs very infrequently once a size threshold (at $R \sim 30$ mm) is reached, and individuals switch to sexual reproduction. *A. insignis* collected in deeper water (>60 m) on the Otago Shelf show similar patterns of fission as those in shallow subtidal and intertidal habitats: smaller individuals ($R = 20\text{--}30$ mm) have regenerating arms while larger ones almost always have six arms of equal length (M.F. Barker, personal observation).

Most individuals of *A. insignis* with $R_0 > 12$ mm, either from the natural population or the fed laboratory treatment, had gonads. In contrast, Emson (1978) reported that sexually mature specimens were rare in a population of *A. polyplax* from Northern New Zealand, and Mladenov and Burke (1994) found a very low occurrence of sexual reproduction among fissiparous sea stars in their review of asexual reproduction in echinoderms. *A. insignis* in our laboratory study were exclusively male and we observed only 2 females out of 38 sea stars

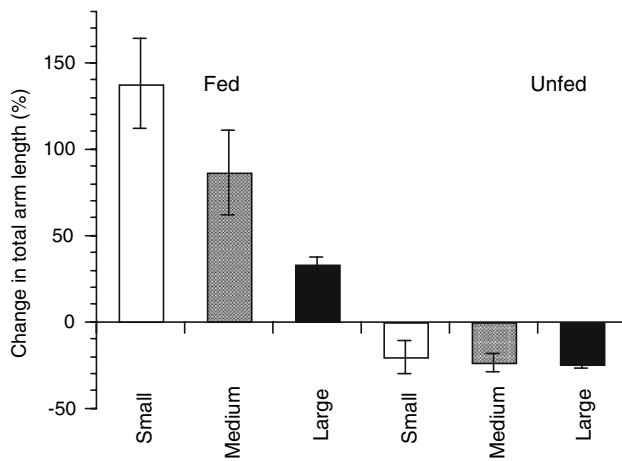


Fig. 8 *Allostichaster insignis*. Percentage change in total arm length (mean \pm SE) of fed ($N = 4-6$) and unfed ($N = 3-6$) animals in small, medium, and large size classes in the laboratory experiment

with macroscopic gonads collected from our field sites. Male-dominated populations also have been reported for other fissiparous sea stars. Rubilar et al. (2005) found only 2 females out of 880 individuals of *Allostichaster capensis* that they examined, and exclusively male populations have been reported for *Coscinasterias tenuispina* in Brazil (Alves et al. 2002) and *Asterina burtoni* in Israel (Achituv and Sher 1991). Crump and Barker (1985) reported a heavily male-biased sex ratio in a population of *C. muricata* in the intertidal zone at our site (Aquarium Point). Sexual differences in rates of fission may result in a preponderance of males observed in populations of fissiparous sea stars. In the laboratory, McGovern (2002) found that males of the fissiparous brittle star *Ophiactis savignyi* were more likely to divide than females, and that fission tended to result in gonad loss in females but not males. She suggested that a greater cost associated with fission could explain why females are less likely to divide.

Fissiparity provides a mechanism for colonization of new habitats through the production of multiple copies of genotypes that are adapted to the local environment (Achituv and Sher 1991). Genetic analyses has confirmed the clonal structure of populations of asexual sea stars [e.g., *Coscinasterias calamaria* (= *muricata*) (Johnson and Threlfall 1987, Sköld et al. 2002); *C. acutispina* (Haramoto et al. 2006), *Asterina burtoni*, (Karako et al. 2002)]. The paucity of settlers, high frequency of fission, and male-biased sex ratio suggest that populations of *A. insignis* in New Zealand are also likely to be highly clonal with relatively low genetic variability. Support for this hypothesis awaits genetic analysis.

Our field and laboratory results indicate that asexual reproduction in *A. insignis* predominantly occurs in small,

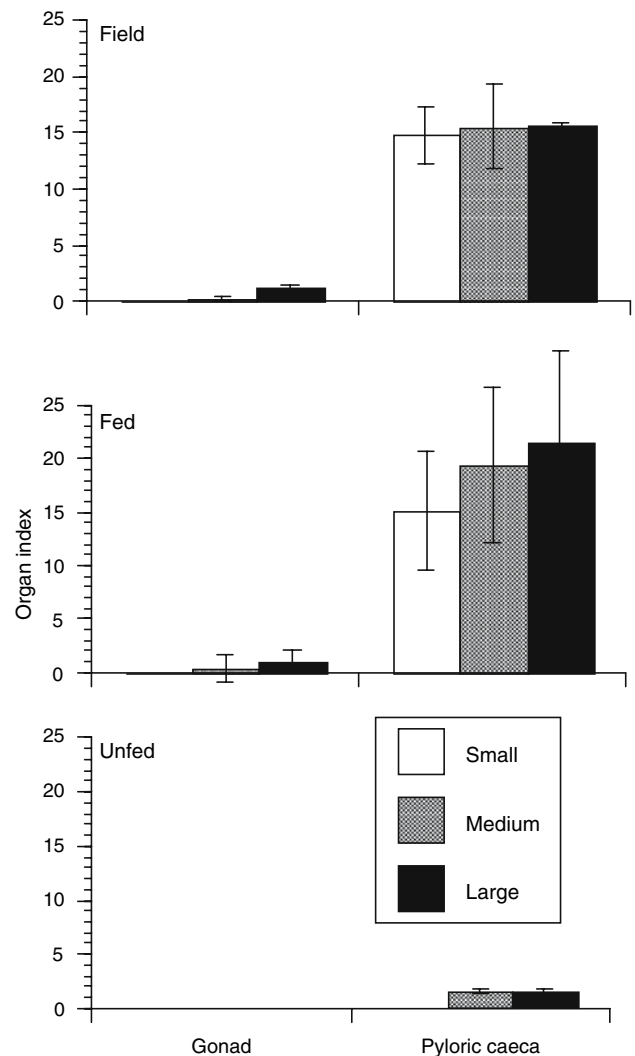


Fig. 9 *Allostichaster insignis*. Gonad and pyloric caeca indices (mean \pm SD) of fed or unfed animals in small, medium, and large size classes in the laboratory experiment ($N = 4-8$, except 14 for medium-fed treatment), and of similar size groups of field-collected animals ($N = 3-7$), at the end of the experiment (February 1991)

well-nourished individuals. Ramets grow gradually through repeated fission and regeneration to a size ($R \sim 20$ mm) at which they begin to switch to sexual reproduction as the dominant reproductive mode. This strategy may enable populations of *A. insignis* to regulate fission rate, and therefore population density, according to the availability of local food resources, and to colonize new habitats via dispersing larvae.

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