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## FEATURE ARTICLE

# Reproductive output and consistency of source populations in the sea star *Pisaster ochraceus*

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ABSTRACT: Although a common goal of marine reserves is to protect areas of high reproductive output, few studies have tested whether these source populations are spatially and temporally consistent. For 6 years between 1995 and 2005, we examined nutrient storage and gonad production in the sea star *Pisaster ochraceus* at 2 sites on the central coast of Oregon, USA. Sea stars accumulated energy in the pyloric caeca during a short season of intensive feeding (May to September). Within a site, the size of the pyloric caeca in the fall accurately predicted reproductive output during the following spring. In accord with hypotheses regarding bottom-up effects, the pyloric caeca were generally larger at the site where mussels were more abundant in the diet, indicating a greater accumulation of surplus energy. However, gonad indices were consistently ~50% lower at this site, suggesting striking differences in allocation to reproduction. This difference between populations was maintained despite marked variation among years in oceanographic conditions and reproductive output. These results suggest that (1) source populations may be consistent spatially, but (2) identifying those sources may be more complex than simply targeting areas with high quality resources and strong bottom-up influences. Rather, predicting patterns of per capita reproductive output may require a more detailed understanding of the causes of spatial variation in allocation to maintenance, growth, and reproduction.

KEY WORDS: Marine reserve · Bottom-up effects · Resource allocation · Reproduction · Marine Protected Area · El Niño

Sea stars *Pisaster ochraceus* feeding on mussels at Strawberry Hill, Oregon, USA.

*Photo: E. Sanford*

## INTRODUCTION

### Source populations and bottom-up effects

A common goal of marine reserve design is the protection of key sources of larval production that may replenish non-protected areas through larval export (Roberts 1997, Carr et al. 2003). However, the quality of reproductive habitat often varies among sites (Crowder et al. 2000, McIntyre & Hutchings 2003, Leslie et al. 2005), and thus identifying sources of larval production has become one consideration in the placement of marine reserves (Quinn et al. 1993, Rogers-Bennett et al. 1995, Sala et al. 2002). In practice, incorporating this

goal into reserve design has proved challenging be-cause (1) spatial variation in the reproductive output of most marine species is poorly known (Roberts 1998, Crowder et al. 2000, Morgan 2001), and (2) prime re-productive habitat may change through time and/or differ among species (Roberts 1998).

A potential solution to these problems is suggested by studies linking oceanographic processes and bot-tom-up effects in marine communities. Recent work demonstrates that oceanographic processes can gener-ate differences in the nearshore abundance of nutri-ents, phytoplankton, particulate food, and invertebrate larvae (see Menge 2000 for a review). Greater inputs at the base of marine food webs often fuel bottom-up increases in the abundance, growth, and reproduction of suspension-feeding invertebrates. These effects may propagate upward by supporting higher densities of consumers (Menge 1992, 2000). Moreover, because oceanographic gradients are often spatially and tem-porally consistent (e.g. related to coastal geomorpho-logy, prevailing winds and currents), sites may vary predictably in the strength of bottom-up forces (Menge et al. 1997, Wing et al. 2003, Leslie et al. 2005). Thus, the problem of siting marine reserves in areas that rep-resent source habitats for a large number of species might be overcome if (1) the availability of high quality resources is a persistent feature of some sites, and (2) bottom-up forces act to increase the abundance and reproductive output of species across multiple trophic levels. This approach to designating areas of protec-tion has recently been suggested for the Galápagos Islands where Witman & Smith (2003) hypothesized that productive upwelling sites may be source habi-tats with enhanced reproductive output of sessile sus-pension-feeding invertebrates, and, potentially, their predators (e.g. other invertebrates and fish).

Although logical, there is relatively little information available to evaluate whether reproductive output is increased among invertebrates and fish living at sites with high resource quality and/or quantity (Morgan 2001). For suspension-feeding invertebrates, perfor-mance may often be linked to pelagic food availability. For example, barnacles and mussels generally grow faster at sites where the abundance of phytoplankton or detritus is consistently higher (Bertness et al. 1991, Menge 1992, Sanford & Menge 2001). Similarly, the reproductive output of barnacles is often higher in areas of high primary productivity (Bertness et al. 1991, Leslie et al. 2005). However, only a handful of studies have tested whether the reproductive output of marine consumers at higher trophic levels is sensitive to resource quality, and these studies have focused mostly on herbivores such as limpets and sea urchins (Rogers-Bennett et al. 1995, Kido & Murray 2003, Wing et al. 2003; but see also McIntyre & Hutchings 2003).

## Study system

Between 1995 and 2005, we examined variation in the reproductive output of the sea star *Pisaster ochraceus* at 2 rocky intertidal sites on the central Ore-gon coast that differed strongly in prey quality. *Pisaster* is a top carnivore that can play a keystone role in main-taining the structure of rocky intertidal communities (Paine 1974, Menge et al. 1994). The abundance of *Pisaster* may be negatively impacted by disease (Eck-ert et al. 1999), parasites (Leighton et al. 1991), preda-tors (Harrold & Pearse 1980), and perhaps human col-lection or disturbance. Because of the community importance of *Pisaster*, management plans for rocky shores along the Pacific coast may wish to identify and protect *Pisaster* populations that could act as reproduc-tive sources to replenish sites impacted by disturbance.

*Pisaster* is dioecious and iteroparous, with broadcast spawning occurring annually during the spring (April to June, depending on latitude and photoperiod; Feder 1956, Farmanfarmaian et al. 1958, Greenfield 1959, Mauzey 1966, Pearse & Eernisse 1982). During periods of heavy feeding, *Pisaster* stores resources in exten-sions of the pyloric stomach called the pyloric caeca. Energy stored in the pyloric caeca appears to be con-verted into gonad production prior to spawning (Mauzey 1966, Harrold & Pearse 1980, Lawrence & Lane 1982). Like many temperate sea stars, *Pisaster* can have a strongly cyclical pattern of feeding activity (Mauzey 1966, Lawrence & Lane 1982). In Washington state and Oregon, the abundance and feeding activity of *Pisaster* in the intertidal zone is concentrated during the spring and summer and greatly reduced during the late fall and winter (Mauzey 1966, Paine 1974, Menge et al. 1994, Navarette & Menge 1996). As feeding activity declines starting in the late fall, the pyloric caeca shrink in size and the gonads grow larger prior to spawning (Mauzey 1966). A seasonal decline in *Pisaster* activity was not observed in Monterey Bay, California (Feder 1970) where the pyloric caeca of *Pisaster* were reported to grow in size along with the gonads until December/January, then decline prior to spawning (Greenfield 1959).

Given the life history of *Pisaster*, reproduction at northern sites may be a function of resources accrued primarily during the season of intensive feeding (spring and summer). Observers of other asteroid spe-cies have noted that individuals with large gonads are sometimes associated with areas of high resource qual-ity (Crump 1971, Barker & Xu 1991). For example, in New Zealand, the sea star *Sclerasterias mollis* had larger pyloric caecum and gonad indices at a site where scallops were the primary prey available than at a site where the diet consisted of gastropods and other small prey (Barker & Xu 1991). When *Pisaster* occur at

sites with abundant mussels and barnacles, the blue mussel *Mytilus trossulus* is the dominant prey in the diet, whereas acorn barnacles are rarely consumed (Sanford 1999, see also Feder 1970). This pattern of prey selection is consistent with data showing that mussels contain more tissue and have a higher caloric value than acorn barnacles (Menge 1972). A logical prediction of these bottom-up considerations is that the reproductive output of *Pisaster* should reflect the frequency of mussels in the diet.

In addition to variation in prey quality, surplus energy available in the pyloric caeca may also be influenced by temperature and other environmental effects on metabolism. For example, interannual variation in water temperature associated with patterns of upwelling may influence *Pisaster* reproduction (Sanford 2002). In laboratory studies, *Pisaster* held at 9°C (simulating continuous upwelling), or in a treatment that fluctuated between 9°C and 12°C every 2 wk (simulating episodic upwelling), had pyloric caecum indices that were 25% greater than sea stars held at a constant 12°C (Sanford 2002). These results raise the question of whether reproductive output is stable in the face of environmental changes, such as those posed by El Niño events and longer-term oceanographic changes.

## Hypotheses

Here, we quantify spatial and temporal variation in the reproductive output of *Pisaster* to explore whether potential source populations are predictable and stable through time. Specifically, we test 4 hypotheses: (1) *Pisaster* accumulate greater stores in the pyloric caeca at sites where the diet includes a greater frequency of high quality prey (mussels versus barnacles); (2) the size of the pyloric caeca at the end of the summer is an accurate predictor of reproductive output during the following spring; (3) interannual variation in the size of the pyloric caeca is reflected in gonad production; (4) nutrient storage and reproductive output are sensitive to interannual variation in oceanographic conditions.

## MATERIALS AND METHODS

**Study sites.** Between 1995 and 2005, we examined nutrient storage and gonad production in *Pisaster ochraceus* at 2 wave-exposed, outer coast sites separated by 34 km on the central coast of Oregon, USA: Strawberry Hill (44° 15′ N, 124° 07′ W) and the South Jetty in Newport, Oregon (44° 36′ N, 124° 04′ W). Strawberry Hill (SH) is composed of extensive rocky

benches, pools, and surge channels (Menge 1992). The Newport South Jetty (NSJ) is a human-made breakwater of large boulders that extends out approximately 1 km WSW from the shore and protects the south side of the entrance to Yaquina Bay. The area studied was on the outside of the jetty, approximately 200 m from shore, and was subject to wave exposure and winter storms comparable to SH (authors' pers. obs.).

Preliminary observations suggested that prey differed markedly between these locations. At SH, patches of the blue mussel *Mytilus trossulus* and gooseneck barnacle *Pollicipes polymerus* were abundant in the low intertidal zone, and beds of the mussel *M. californianus* dominated the mid intertidal zone (Menge et al. 1994). Previous work identified SH as a site with seasonally high phytoplankton productivity and high rates of mussel recruitment and growth (Menge 1992, Menge et al. 1997). Mussels and gooseneck barnacles were uncommon at NSJ. Here, low intertidal surfaces were dominated by algal turf, coralline algae, and the clonal anemone *Anthopleura elegantissima*, and the most abundant prey were the acorn barnacles *Balanus glandula* and *Chthamalus dalli* on mid intertidal boulder faces.

**Quantification of sea star diet.** A permanent sampling area was established at both SH and NSJ consisting of ~300 m² of low intertidal rocky habitat. Each area was surrounded by deep channels and sand that likely discouraged large-scale movements of sea stars. We quantified sea star diet within the sampling areas during 5 periods (July 1995, May 1996, August 1996, May 2003, and April 2005) by placing two 30 m transects parallel to the water. We examined the first 100 sea stars within 1m of each transect and noted all prey items that were being consumed. Consumed prey included (1) those that sea stars were actively feeding on (with the sea star's stomach everted), or (2) those that had been recently eaten (with remains and shells present at the edge of the sea star's mouth). If a sea star was feeding on one or more mussels, we measured the shell length of the largest mussel being consumed. We did not attempt to quantify between-site differences in the total amount of food consumed by *Pisaster* as this would have required frequent sampling when sea stars were submerged. The high wave energy of these sites made it impossible to sample sea stars at high tide.

**Seasonal variation in the intertidal abundance of sea stars.** Between May 1995 and February 1998, we recorded seasonal variation in the density of *Pisaster ochraceus* in permanently marked rectangular plots (mean area ± SE = 3.49 ± 0.30 m²). Plots were located in the sampling area at SH (n = 11) and in an area located 1 km to the south (Bob Creek Wayside, n = 15). Plots were positioned on horizontal surfaces at +0.7 to

+1.2 m above mean low low water (MLLW), just below the lower edge of the mussel bed. This is the tidal range where *Pisaster* were most commonly observed foraging at our sites (authors' unpubl. data). We recorded the density of sea stars within these plots every 2 wk during the spring and summer, and every 4 to 6 wk during the remainder of the year (n = 62 dates). We did not quantify sea star density at NSJ on a routine basis because the irregular boulders were poorly suited for large, horizontal plots, and because wave swell made the jetty hazardous to access on a frequent schedule, especially during the fall and winter.

**Sea star dissections.** To characterize seasonal cycles in the pyloric caeca and gonads, we collected *Pisaster* at SH and NSJ during the first spring tide series of every other month between August 1995 and August 1997. To determine the time of spawning with greater precision, collections were also made during both May and June of 1996, 1997, and 1998. During the later part of this study, collections were made twice a year to capture annual peaks in the pyloric caeca (Fall 1997, 1998, 2002, and 2004) and gonads (May 1998, 1999, 2003, 2005). On each date, 12 individuals per site were collected haphazardly from the sampling area, weighed in the field using a digital balance, and retained if their wet weight fell within the range of 170 to 260 g. This is the most common size class present at many sites along the central Oregon coast (Menge et al. 1994, E. Sanford unpubl. data). *Pisaster* reaches sexual maturity at 70 to 90 g wet weight (Menge 1975).

Following collection, sea stars were held in seawater tables at Hatfield Marine Science Center in Newport, Oregon, for 24 h, and then dissected following established methods (Farmanfarmaian et al. 1958, Mauzey 1966). Prior to dissection, sea stars were anesthetized for 15 to 20 min in an isotonic solution of $MgCl_2$ and seawater. Radial cuts along the aboral surface of each arm were made using scissors (Soft Touch Micro-Tip Scissors, Fiskars), and the gonads and pyloric caeca were removed. The eviscerated sea star was weighed and the removed organs were blotted on paper towels for 15 min to remove excess water. The volume of the pyloric caeca and gonads were determined by their displacement of known volumes of water in a graduated cylinder (Mauzey 1966). Following previous studies (Lawrence & Lane 1982), the gonad and pyloric caecum indices were defined as the ratio of that organ's volume to eviscerated body weight ×100. The specific gravity of the pyloric caeca, gonads, and sea water are essentially equivalent (Mauzey 1966), so that indices determined with either organ wet weight or volume are comparable (Lawrence & Lane 1982). The peak gonad index is assumed to accurately reflect reproductive output in asteroids because non-gametogenic material is minimal when the gonads are fully mature (Lawrence 1985).

**Interannual variation in water temperature and mussel recruitment.** Long-term studies at one of our sites (SH) provided an opportunity to test whether the reproductive output of *Pisaster* responded to interannual differences in water temperature and/or mussel recruitment. Two data-loggers (Optic Stow-Away or TidbiT loggers, Onset Computer) were attached in the low intertidal zone at SH and recorded temperature every 30 min during the months when *Pisaster* was accumulating energy in the pyloric caeca (May through August). These are also the primary months when coastal upwelling occurs along the central Oregon coast. For each high tide, we calculated the mean of all readings taken during a 4 h interval centered around each high tide (as estimated from NOAA tide charts).

Mussel recruit collectors were also attached in the low intertidal zone within the same sampling area at SH. Collectors were plastic mesh balls (SOS Tuffy pads, Clorox) deployed monthly (n = 5 mo$^{-1}$) throughout this study as part of a long-term monitoring program (Menge 1992, Barth et al. 2007). Collectors were returned to the laboratory and mussel recruits were counted under a dissecting microscope. Newly settled mussels could not be identified reliably to species and thus were grouped as *Mytilus* spp. However, previous studies indicate that blue mussels *Mytilus trossulus* settle abundantly in the low intertidal zone at SH during the fall, and patches of juvenile mussels (10 to 25 mm) are conspicuous by winter (Menge et al. 1994, Navarrete & Menge 1996). These patches are the major food source for *Pisaster* at SH (see 'Results'). To focus on the primary settlement season of *M. trossulus*, we analyzed collector data for the period of July to December of each year.

**Statistical analysis.** Organ indices were analyzed using analysis of variance (ANOVA). Within the range of individuals sampled (170 to 260 g wet weight), least squares linear regressions of condition (gonad volume, peak gonad index, pyloric caeca volume, peak pyloric caecum index) on eviscerated body weight were non-significant (p > 0.20 for most Site × Year combinations). Thus, we did not use sea star weight as a covariate in our analyses. Variation in the fall pyloric caecum index was examined using ANOVA with Site and Year as fixed factors. Pyloric caecum indices were log transformed prior to analysis to improve homogeneity of variances. Gonad indices from May of each year were analyzed in a separate ANOVA with Site, Year, and Sex as fixed factors. These data met the assumptions of ANOVA reasonably well and were not transformed. To test whether organ indices varied between sites within specific years, we conducted separate *t*-tests using a Bonferroni adjusted critical $\alpha$ = 0.0083 to control for multiple comparisons across the 6 yr.

Multiple linear regression analysis was used to test whether internannual variation in the pyloric caecum index at SH was a function of mussel recruitment and water temperature at that site. Mussel recruitment was calculated as the mean number of recruits per day per collector during the months of July to December (prior to *Pisaster*'s primary feeding season, May to August). Three explanatory variables were tested in separate models as indicators of interannual variation in water temperature between May and August: the proportion of high tides <10°C, between 10 and 12°C, and >12°C. All analyses were performed using JMP IN (version 5.1.2, SAS).

## RESULTS

### Between-site differences in diet

*Pisaster* diet differed markedly between Strawberry Hill and the Newport South Jetty (Fig. 1). Sea star diets within a site were consistent through time and thus diet data were pooled across years. At SH, sea stars fed almost exclusively on the blue mussel *Mytilus trossulus* and the gooseneck barnacle *Pollicipes polymerus*. In contrast, 83% of feeding sea stars at NSJ preyed on the acorn barnacles *Balanus glandula*, *Chthamalus dalli*, and *Semibalanus cariosus*. Although some sea stars at NSJ also fed on *M. trossulus*, these mussels were generally recent recruits that were attached to the shells of barnacles. These recruits were smaller than the mussels consumed at SH (mean shell length ± SE = 8.55 ± 0.32 vs. 20.18 ± 0.41 mm; *t*-test, $t_{513}$ = 19.8, p < 0.001), and were probably consumed incidentally with barnacles.

### Seasonal variation in the intertidal activity of *Pisaster*

The density of *Pisaster* in intertidal plots at SH and an adjacent location (Bob Creek Wayside) was strongly seasonal during the 3 yr of observation (Fig. 2). Data from these locations were pooled because all plots were located within 1 km of the shore and displayed the same seasonal trends in sea star abundance. From May to September, the mean density ± SE of *Pisaster* was 4.77 ± 0.16 ind. m$^{-2}$. From November to March, the mean density was 77% lower (1.11 ± 0.06 ind. m$^{-2}$). A similar seasonal decline in *Pisaster* density was noted at NSJ during the regular collection of sea stars for dissection
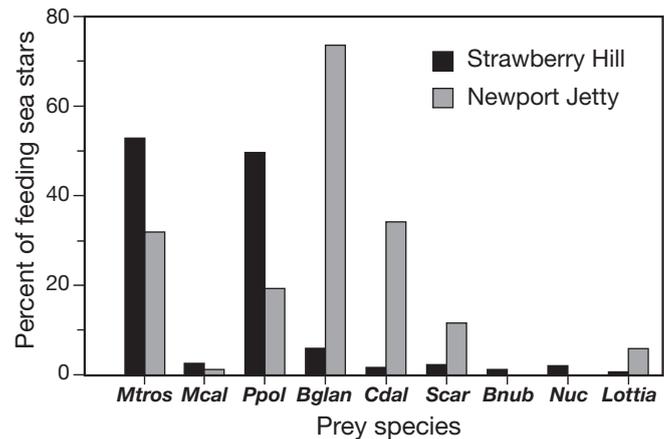


Fig. 1. *Pisaster ochraceus.* Diet of *P. ochraceus* at Strawberry Hill and Newport South Jetty, Oregon, USA showing the percent of sea stars feeding on prey species. For mussels: *Mtros = Mytilus trossulus*, *Mcal = M. californianus*; for barnacles: *Ppol = Pollicipes polymerus*, *Bglan = Balanus glandula*, *Cdal = Chthamalus dalli*, *Scar = Semibalanus cariosus*, *Bnub = Balanus nubilus*; for whelks: *Nuc = Nucella canaliculata* and *N. ostrina*; and for limpets: *Lottia = Lottia* spp. Diets are based on the pooled data for all feeding sea stars sampled at Strawberry Hill (n = 618) and the Newport Jetty (n = 607) between 1995 and 2005 (see 'Materials and Methods' for sampling dates). The cumulative percent at each site exceeds 100% because *Pisaster* often feeds on more than one prey species at a time

(authors' pers obs). Temporary declines in *Pisaster* density during the spring and summer (Fig. 2) were frequently associated with cold water upwelling events, during which sea stars become inactive in low zone channels and shallow subtidal water (Sanford 1999).
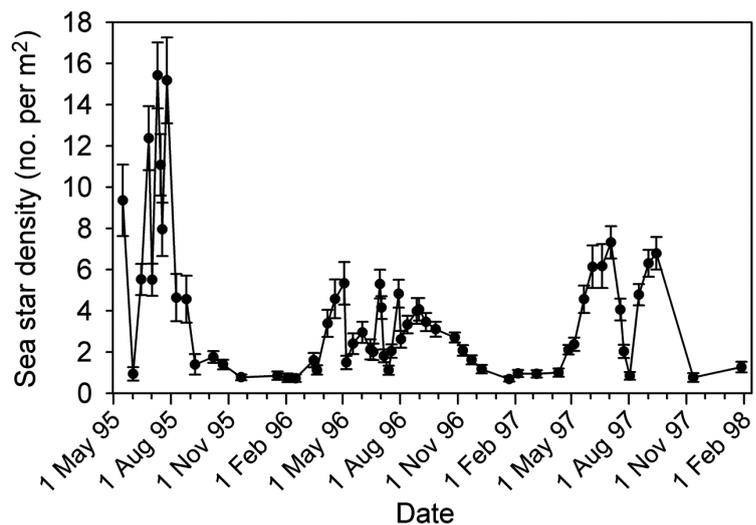


Fig. 2. *Pisaster ochraceus.* Seasonal variation in the density of *P. ochraceus* (mean ± SE) in permanently marked, low intertidal plots (n = 26) along 1 km of shore at Strawberry Hill/ Bob Creek Wayside
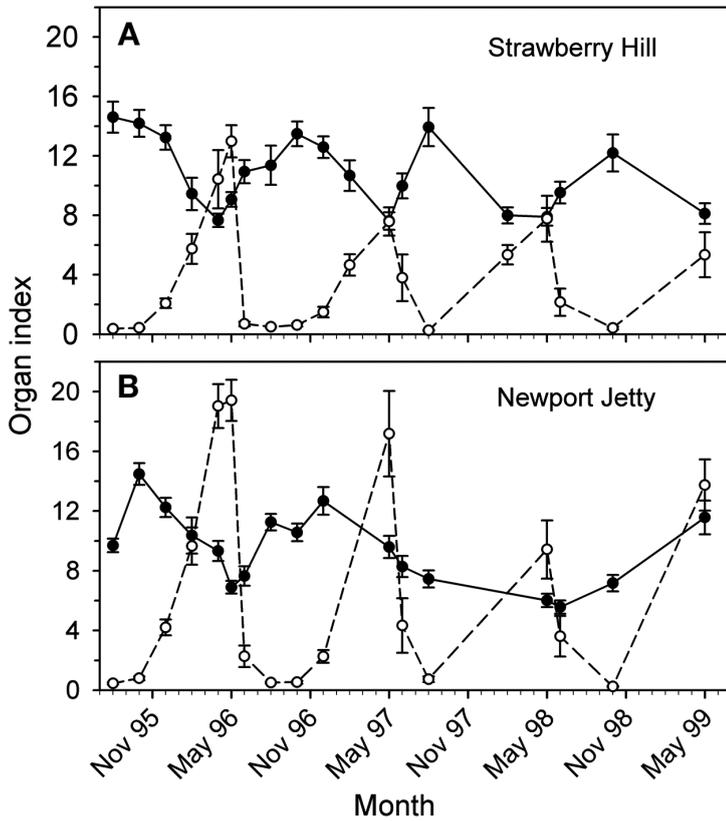
Fig. 3. *Pisaster ochraceus.* Cycles in pyloric caecum (solid line) and gonad indices (dashed line) on the central Oregon coast. Each point is the mean (± SE) of 12 sea stars collected at (A) Strawberry Hill and (B) the Newport South Jetty between August 1995 and May 1999

## Spatial and temporal variation in pyloric caecum and gonad indices

At both sites, changes in pyloric caecum and gonad size were cyclical and inversely related (Fig. 3). The pyloric caecum index increased steadily over a 5 mo period (May to September), peaked in the early fall, and then shrank in size over winter as gonads were produced. Two exceptions to this general pattern occurred at NSJ: no increase in the pyloric caecum index was observed in summer 1997, and in May 1999 the pyloric caecum index was uncharacteristically high for this season (Fig. 3B).

At both sites, the gonad index peaked in early May and most individuals spawned during the period

Fig. 4. *Pisaster ochraceus.* Variation in *Pisaster* condition between Strawberry Hill and the Newport South Jetty. Bars are means (+SE) for 12 sea stars per site; (✳) significant difference between sites (*t*-test, Bonferroni corrected p < 0.0083). (A) Peak pyloric caecum index recorded during fall of each year. (B) Peak gonad index recorded in May of each subsequent year

between our collections of 1 May and 10 June. *Pisaster* were observed spawning in the field at SH and nearby sites only during this period (including 17 May 1995, 2 May 1996, 4 May 1996, 1 June 1996, 17 May 2003, 21 May 2004). Of the sea stars sampled at SH and NSJ, 96% had spawned by 10 June 1996, and 75% had spawned by 10 June 1997 and 10 June 1998. Similarly, collections at SH on 19 May 2003 contained no ripe individuals (L. Petes unpubl. data). For the remaining 2 yr of the study, we assume that our samples in early May 1999 and 2005 also captured the peak gonad index, although we did not sample in early June of those years to confirm that spawning had occurred.

As predicted based on the greater prevalence of mussels in the diet at SH, the size of the pyloric caeca in the fall was generally greater at SH than at NSJ (Fig. 4A; Table 1, Site, p < 0.001). Surprisingly, despite having smaller pyloric caeca than SH sea stars, individuals at NSJ produced larger gonads in most years (Fig. 4B). At both sites, the size of the pyloric caecum index in the fall was a good predictor of gonad production during the following spring (Fig. 5). However, for any given value of the pyloric caecum index, NSJ sea stars had approximately double the gonad production (Fig. 5).

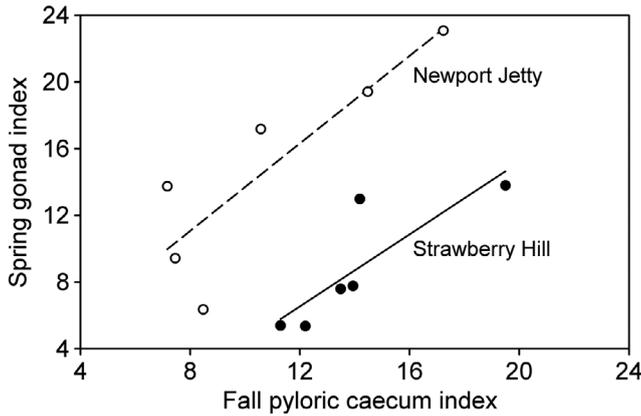Gonad production varied markedly among years (Fig. 4B; Table 2, Year, p < 0.001). For
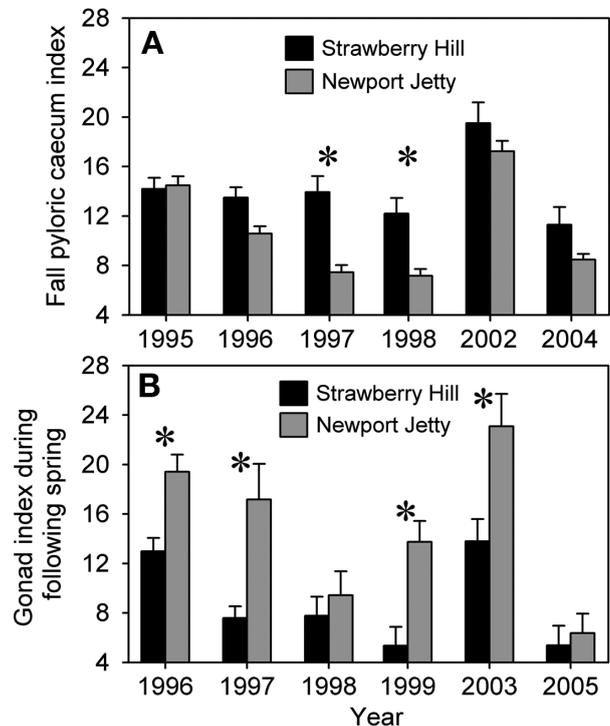
Fig. 5. *Pisaster ochraceus.* Relationship between size of the pyloric caeca during the fall and gonad production during the following spring. Each point represents 1 yr at Strawberry Hill (SH, ●) and the Newport South Jetty (NSJ, ○). Separate linear regressions are plotted for each site; SH: gonad = (1.081 × caecum) − 6.43, $R^2$ = 0.70, p = 0.038; for NSJ: gonad = (1.312 × caecum) + 0.570, $R^2$ = 0.74, p = 0.028

example, at NSJ, per capita gonad production in spring 2003 was 3.6 times greater than in spring 2005 (Fig. 4B). Similarly, at SH, per capita gonad production in spring 2003 was 2.6 times greater than in spring 2005. Nevertheless, gonad production was consistently greater at NSJ (Table 2, Site, p < 0.001; Site × Year, p > 0.05). There was no evidence that the spring gonad index varied between male and female sea stars (Sex, p > 0.10).

## Influence of water temperature and mussel recruitment

Long-term monitoring at SH allowed us to test whether the size of the pyloric caeca attained by the end of the summer feeding season was related to variation in water temperature and/or mussel recruitment at this site. Water temperatures during the period May to August differed strongly among years in association with variation in the frequency and intensity of coastal upwelling (Table 3). Upwelling conditions (indicated by water temperatures <10°C along the central Oregon coast) are frequently suppressed during El Niño years. The 1997–98 El Niño was the strongest of the century in Oregon waters (Smith et al. 2001), and cool water temperatures were uncommon at SH during summer 1997. Weaker El Niño conditions also occurred during summer 2004. In contrast, 1996 and

2002 were marked by strong upwelling seasons with a much greater frequency of cold-water events (Table 3).

As an indicator of interannual variation in *Mytilus trossulus* abundance, we examined mean mussel recruitment to artificial collectors deployed monthly during the period July to December. At SH, mussels recruit to the low zone primarily during this period and become the main prey for *Pisaster* during the following spring/summer (Menge et al. 1994, Navarrete & Menge 1996). During late 1994, 1995, 1996, and 1997, mussel recruitment was moderate, typically ~20 mussel recruits d$^{-1}$ collector$^{-1}$ (Fig. 6). Beginning in the late 1990s there was a massive increase in *Mytilus* recruitment at SH,

Table 1. Analysis of variance (ANOVA) of the effects of Site and Year on the fall pyloric caecum index for *Pisaster*. The response variable was log transformed prior to analysis. p-values in bold are significant (p < 0.05)

| Source | df | SS | F | p |
|---|---|---|---|---|
| Site | 1 | 2.90 | 41.5 | **<0.001** |
| Year | 5 | 8.91 | 25.5 | **<0.001** |
| Site × Year | 5 | 1.92 | 5.5 | **<0.001** |
| Residuals | 138 | 9.64 | | |
| Total | 149 | 23.37 | | |

Table 2. Analysis of variance (ANOVA) of the effects of Site, Year, and Sex on the spring gonad index for *Pisaster*

| Source | df | SS | F | p |
|---|---|---|---|---|
| Site | 1 | 1217.2 | 31.8 | **<0.001** |
| Year | 5 | 2875.3 | 15.0 | **<0.001** |
| Site × Year | 5 | 421.4 | 2.2 | 0.058 |
| Sex | 1 | 103.8 | 2.7 | 0.102 |
| Residuals | 131 | 5014.2 | | |
| Total | 143 | 9631.9 | | |

Table 3. Interannual variation in water temperature, mussel recruitment, and pyloric caecum indices for *Pisaster* at Strawberry Hill, Oregon. Table shows percent of high tides with water temperature <10°C (characteristic of upwelling), 10–12°C, or >12°C during the period May to August (the peak feeding season for *Pisaster*). Mussel recruitment is mean number of *Mytilus* recruits per collector during the period July to December of the year (i.e. 1994, 1995, etc.) prior to the primary season of *Pisaster* activity (spring/summer). Final column shows peak pyloric caecum index attained during early fall

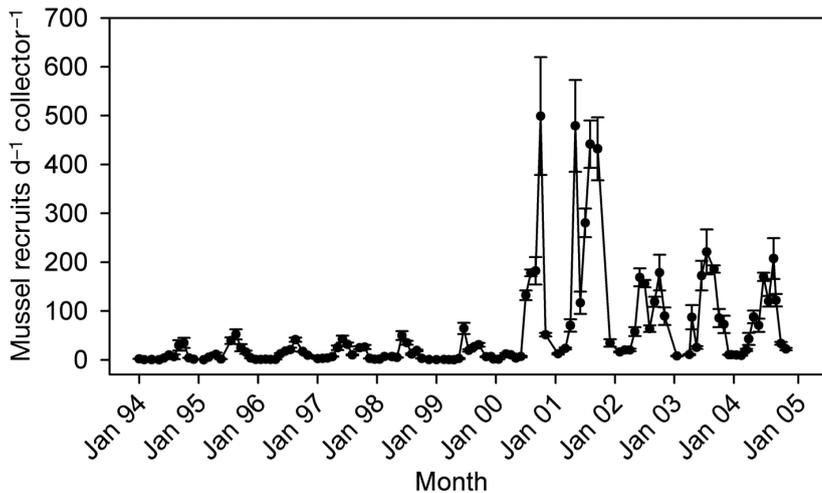| Year | High tide temperatures (%) | | | Mussel recruitment | Pyloric caecum |
| | <10°C | 10–12°C | >12°C | (ind. d$^{-1}$) (±SE) | index |
|---|---|---|---|---|---|
| 1995 | 23.5 | 46.9 | 29.6 | 15.2 ± 4.1 | 14.2 |
| 1996 | 48.5 | 31.4 | 20.1 | 27.2 ± 4.4 | 13.5 |
| 1997 | 13.8 | 33.5 | 52.7 | 22.2 ± 3.0 | 13.9 |
| 1998 | 29.6 | 48.3 | 22.1 | 19.4 ± 2.6 | 12.2 |
| 2002 | 64.8 | 23.2 | 12.0 | 297.3 ± 42.6 | 19.5 |
| 2004 | 23.7 | 36.9 | 39.4 | 115.1 ± 18.5 | 11.3 |

Fig. 6. *Mytilus* spp. Monthly mussel settlement at Strawberry Hill, 1994 to 2004. Data are mean (± SE) number of mussel recruits per day from collectors (n = 5 mo$^{-1}$) attached in the low intertidal zone. Collectors were deployed in the same area from which *Pisaster* was sampled

perhaps linked to a temporary, 4 yr shift to the cold phase of the Pacific Decadal Oscillation (PDO) (B. A. Menge, J. Luchenco, F. Chan unpubl. data). Mussel abundance in collectors was an order of magnitude higher during the 2001 and 2003 recruitment seasons than during the 1994 to 1997 recruitment seasons. During the period July to December 2001, mean recruitment was nearly 300 mussel recruits d$^{-1}$ collector$^{-1}$ (Table 3).

Despite strong variation in water temperature and mussel recruitment, the peak pyloric caecum index at SH varied little among years; there was no significant variation in the pyloric caecum index among fall 1995, 1996, 1997, 1998, 2004 (Fig. 4A). Severe El Niño conditions during summer 1997 did not appear to have strong impacts on either the size of the pyloric caeca or subsequent reproduction during spring 1998. However, the pyloric caecum index in fall 2002 was 37 to 73% greater than during the other 5 yr of this study. In multiple linear regression models, neither mussel recruitment (p > 0.20) nor water temperature (proportion of high tides <10°C, 10 to 12°C, or >12°C; p > 0.50 in each case) explained interannual variation in the pyloric caecum index at SH. The lack of a statistical relationship was expected because there was little variation in the pyloric caecum index at SH, except for fall 2002. However, the unusually large pyloric caeca of 2002 was coincident with a combination of massive mussel recruitment during late 2001 and frequent cold water events during summer 2002 (Table 3). The large pyloric caecum index observed in fall 2002 occurred at both sites and was followed by a per capita reproductive output that was up to 3.6 times greater than during a poor reproduction year (e.g. compare spring 2003 with spring 2005; Fig. 4B).

## DISCUSSION

### Bottom-up effects and interannual variation in reproductive output

Consistent with the hypothesized bottom-up effect of mussels, *Pisaster* at SH often developed larger pyloric caeca than sea stars at NSJ (Fig. 4A). Mussels were the dominant prey in the diet of sea stars at SH, whereas less profitable prey (i.e. acorn barnacles; Menge 1972) were the primary prey consumed at NSJ (Fig. 1). At both sites, the pyloric caecum index at the end of the summer feeding season predicted reproductive output during the following spring (Fig. 5). As observed in previous studies of *Pisaster* (Feder 1956, Farmanfarmaian et al. 1958, Greenfield 1959, Mauzey 1966, Pearse & Eernisse 1982), there was generally a cyclical, inverse relationship between the size of the pyloric caeca and the gonads. Based on this pattern, earlier authors inferred that surplus energy stored in the pyloric caeca was directed toward gonad production during the winter (Farmanfarmaian et al. 1958, Mauzey 1966). Here, we demonstrate that there is a predictive relationship between the size of the pyloric caeca in the fall and gonad volume during the following spring (Fig. 5). Thus, reproductive output at our sites appears to be determined primarily by the ability of *Pisaster* to accrue resources during a period of intensive feeding in the intertidal zone (between spring and early fall). As in Washington state (Mauzey 1966, Paine 1974), the intertidal abundance and activity of *Pisaster* at these sites declined sharply in the late fall and winter. A similar pattern has been noted previously for *Pisaster* in Oregon (Menge et al. 1994, Navarrete & Menge 1996), but not for central California where *Pisaster* activity was reported to show no seasonal decline (Feder 1970).

Reproductive output varied by a factor of 2.5 to 3.6 among years, with productive years and poor years. In previous laboratory studies, water temperature was found to have an important influence on the feeding of *Pisaster* and on the size of the pyloric caeca (Sanford 2002). When raised on an ad libitum diet, sea stars held at 9°C generally consumed fewer mussels but developed pyloric caeca that were 25% larger than those held at 12°C, suggesting that individuals experiencing the cool water temperatures associated with upwelling events may benefit from reduced metabolic costs (Sanford 2002). In our analyses of field collected *Pisaster* there was no evidence that interannual variation in water temperature alone was associated with variation

in the size of the pyloric caeca. For example, the pyloric caecum index at SH differed little following summer 1996 (a cool year) and summer 1997 (a warm year during a strong El Niño event, Table 3). However, the pyloric caecum index increased substantially at SH during 2002 in association with unusually cool water temperatures and a striking increase in mussel settlement. These changes appeared to be linked with the PDO, which switched from a warm phase to a cool phase during 1999 to 2002 (B. A. Menge, J. Lubchenco, F. Chan unpubl. data).

Many sea stars, including *Pisaster*, are thought to have relatively low annual recruitment of larvae, punctuated by unusually strong settlement events in some years (Sewell & Watson 1993, Witman et al. 2003, Blanchette et al. 2005). The observation that gonad production varied sharply among years may provide a partial explanation for annual variation in sea star settlement. Surveys of *Pisaster* size structure at SH and NSJ showed a much greater frequency of small *Pisaster* (<50 g wet weight) in 2003 and 2005, relative to 1995 and 1996 (E. Sanford unpubl. data). This suggests that oceanographic conditions during the period 2000 to 2002 may have been conducive to both high reproductive output of *Pisaster* and subsequent recruitment of juveniles onshore. Although asteroids generally have a long larval phase with high dispersal potential, previous studies suggest that in some years favorable conditions for sea star reproduction may occur over regional scales (Witman et al. 2003, Blanchette et al. 2005). For example, Witman et al. (2003) observed unprecedented recruitment of the sea star *Asterias* in the year following a massive subtidal recruitment of mussels to the Gulf of Maine, USA. The authors hypothesized that the unusually strong recruitment of this sea star represented a bottom-up effect of enhanced food supply on the reproductive condition of *Asterias*.

## Between-site variation in gonad production and energy allocation

An unexpected result of our study was that sea stars at the site with higher prey quality (SH) failed to produce larger gonads. Although sea stars at SH generally had larger pyloric caeca, NSJ sea stars produced twice as much gonadal tissue for a given size of pyloric caeca (Fig. 5). The difference in gonad production was apparent in the winter (e.g. December 1995 and February 1996; Fig. 3) indicating that the smaller May gonad index at SH did not arise from partial or early spawning at that site.

We propose 2 potential hypotheses to explain the between-site variation in reproductive output. First,

*Pisaster* at NSJ and SH may have experienced different abiotic conditions during the winter that led to greater gonad production at NSJ. Both sites are exposed outer coast sites that are subjected to storms and considerable wave swell during the winter. However, NSJ is composed of large boulders, and the spaces among boulders could have provided *Pisaster* with a greater refuge from wave stress than at SH. If sea stars at NSJ expended less energy on locomotion and maintenance during the winter, they may have devoted more stored energy to gonad production.

Similarly, *Pisaster* at NSJ may have continued feeding during the winter in the subtidal recesses of the jetty. There is some evidence that sea stars can transfer ingested nutrients directly to the developing gonads without involvement of the pyloric caeca (Beijnink & Voogt 1984). Thus, if sea stars consumed greater subtidal resources during the winter months at NSJ than at SH, these extra resources may have been devoted to increased gonad production without any changes in the pyloric caecum index. During the late fall and winter, *Pisaster* in Oregon and Washington state become less active and retreat to the very low intertidal or shallow subtidal zone (Mauzey 1966, Paine 1974, Menge 1992, Menge et al. 1994, Navarrete & Menge 1996). This seasonal change in distribution was observed at both SH and NSJ (Fig. 2; authors' pers. obs.). Although feeding activity is reduced during the winter months, some feeding continues throughout the winter (Mauzey 1966, Navarrete & Menge 1996, authors' unpubl. data). Unfortunately, the high wave energy of our sites made it dangerous to collect data on the diet and activity of *Pisaster* in the shallow subtidal zone, particularly during the winter. However, the ability of the fall pyloric caecum index to predict peak gonad production (independent of any information on winter feeding; Fig. 5), suggests that energy stored during the summer feeding season is the major determinant of annual reproductive output in this species.

An alternative hypothesis to explain the between-site differences in reproductive output is that sea stars at NSJ may have allocated more energy to reproduction than individuals at SH. In echinoderms, energy may be allocated to maintenance, growth, and reproduction, and the pattern of allocation may be a complex function of demographic and environmental factors (Harrold & Pearse 1980, Ebert 1982, Lawrence 1985, 1987). Differences between sites in allocation to reproduction could have resulted if we sampled sea stars that were different ages. Although we restricted sampling of *Pisaster* to a narrow size range (170 to 260 g wet weight), it is possible that sea stars of this size were older at NSJ than at SH. Unfortunately, most sea stars cannot be aged based on size or skeletal structures (but see Stump & Lucas 1990), and individ-

uals are notoriously difficult to tag. However, *Pisaster* are estimated to live longer than 20 yr (Menge 1975). It is possible that sea stars at SH grow faster than those at NSJ because of the greater availability of *Mytilus trossulus*. In an earlier experiment, *Pisaster* maintained in laboratory tanks on an ad libitum diet of *M. trossulus* doubled their wet weight in 2 mo (from ~130 to 260 g) (Sanford 2002). At NSJ, where *Pisaster* feeds primarily on less productive prey (i.e. acorn barnacles; Menge 1972, 1975), individuals may take longer to reach a given size than their counterparts at SH.

Empirical studies of marine invertebrates suggest that younger individuals often allocate greater resources to somatic growth than reproduction (Thompson 1979, Kettle & Lucas 1987). As individuals age, resources are increasingly channeled to reproduction, and the gonad index increases. An age-related increase in reproductive effort has been documented in echinoderms, including the crown-of-thorns sea star *Acanathaster planci* and some echinoids (Thompson 1979, Lawrence 1985, Kettle & Lucas 1987, Stump & Lucas 1990). This life history strategy may be a response to selection imposed by the disadvantages of small body size (e.g. reduced competitive ability, reduced foraging efficiency, and/or greater predation on small individuals). Mortality in *Pisaster* is estimated to be high in juvenile sea stars (Menge 1975, Sewell & Watson 1993), suggesting that younger individuals may be selected to direct more resources towards somatic growth than reproduction.

Theoretical work also suggests that reproductive effort may increase with age in iteroparous animals with reproductive senility (Roff 2002). Older individuals may be selected to invest more in current fecundity because the expectation of future offspring production decreases with age (Pianka & Parker 1975). Although there are empirical data to support this prediction in vertebrate ectotherms (Roff 2002, McIntyre & Hutchings 2003), there is less information about age-specific fecundity in invertebrates (but see Thompson 1979, Kettle & Lucas 1987, Stump & Lucas 1990). Reproductive senility has been observed in sea stars (Lucas 1984) and some sea urchins (Lawrence 1987, but see Ebert & Southon 2003) but has not been studied in *Pisaster*. Further studies are needed to explore whether between-site variation in age structure may influence patterns of reproductive allocation.

### Implications for identifying source populations

The potential for a site to act as a reproductive source may depend on a variety of factors including population density, age and size structure, total population size, per capita reproductive output, and local

hydrodynamics (Denny et al. 1992, Levitan et al. 1992, Quinn et al. 1993, Kido & Murray 2003, Wing et al. 2003, Leslie et al. 2005). Overall, our results suggest that *Pisaster* at NSJ had consistently higher per capita reproduction than those at SH, despite considerable variation among years in oceanographic conditions and reproductive output. This result lends support to the idea that reproductive source populations may be spatially and temporally consistent for a given species. Siting marine reserves to protect such populations may help replenish non-protected areas through larval export (Rogers-Bennett et al. 1995, Roberts 1997, Crowder et al. 2000). However, in our study, the population with greater per capita reproductive output was found at the site with lower quality prey. This counter-intuitive result suggests that identifying source populations may be more complex than simply protecting sites with high quality resources and strong bottom-up influences. Rather, predicting patterns of per capita reproductive output may require a more detailed understanding of how demographic and environmental factors influence the allocation of resources to maintenance, growth, and reproduction. The importance of these factors may be particularly strong for long-lived iteroparous consumers.

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