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Massive crab recruitment events to the shallow subtidal zone

High-density and temporally pulsed propagule recruitment strategies are common in many plants (e.g., masting, Kelly 1994), and both terrestrial (e.g., cicada emergence; Williams and Simon 1995) and marine invertebrates (reviewed in Caley et al. 1996). The extent and effects of recruitment pulses on population dynamics of the species involved and their subsidy to local predator populations are broadly appreciated (Karban 1982, Byström 2006). While well documented for many sessile marine invertebrates, such as barnacles (e.g., Strathmann and Branscomb 1979), curiously, such mass-recruitment events to the marine benthos have not, to our knowledge, been described for mobile consumer species like crabs. Large, episodic influxes of new settlers could have very strong, yet under-appreciated, impacts on the communities in which they land, both as a source of prey and as predators on local organisms.

During a SCUBA dive at Port Orford, Oregon, USA on 19 April 2016, Galloway observed a remarkably dense benthic aggregation of recently settled *Cancer* (*Metacarcinus*) *magister* megalopae, the final larval stage of decapod crustaceans, as well as new recruits (first-instar settlers). Between 7 and 13 m depth (the deepest descent) and throughout the 45-min dive, every surface of the rocky reef, including sessile invertebrates, algae, vertical rock walls, and cobbles, in an estimated 100-m^2 area, was completely covered with new recruits. The recruits were stacked upon each other, several individuals deep. Without a camera during this dive, Galloway collected a handful of crabs and photographed them on the shore to document their size (Appendix S1). Based on the carapace width of the recruits (mean = 7.1 mm, SD = 0.69, n = 12), we estimated a density of ~22,000 crabs/m^2 (one layer of crabs), and densities may have been as high as ~65,000 crabs/m^2 (three layers of crabs). There were no recruits observed at this site on an earlier dive on 4 April 2016.

Observations by an Oregon Department of Fish and Wildlife (ODFW) biologist (J. Watson, *personal communication*) were consistent with ours. Two days before, Watson was sampling demersal rockfish using hook and line near Depoe Bay, Oregon (250 km to the north), and reported that an usually large proportion of rockfish caught, particularly black rockfish (*Sebastes melanops*), were regurgitating newly settled Dungeness crabs. On a SCUBA dive at the original dive site (Graveyard Point; 42.73837° N, 124.49938° W) 23 d later (13 May 2016), there were still dense aggregations of new recruits, with densities of ~5,000–11,000 crabs/m^2 (Fig. 1a), but the recruits were now located at the interface between the rocky reef and the cobble/sandy bottom. On this same day, ODFW biologists were conducting remote operated vehicle (ROV) surveys near the Redfish Rocks Marine Reserve, ~7 km south of the Port Orford dive site, and also observed dense aggregations of new recruits (~3,000–7,000 crabs/m^2; Video S1).

On nine subsequent dive surveys at rocky reefs in the Port Orford area (sites within a 20-km^2 area), and as late as 31 August 2016, juvenile age 0+ crabs (~6–13 mm carapace width) were observed in groups in all habitat types, including vertical walls, at densities ranging from

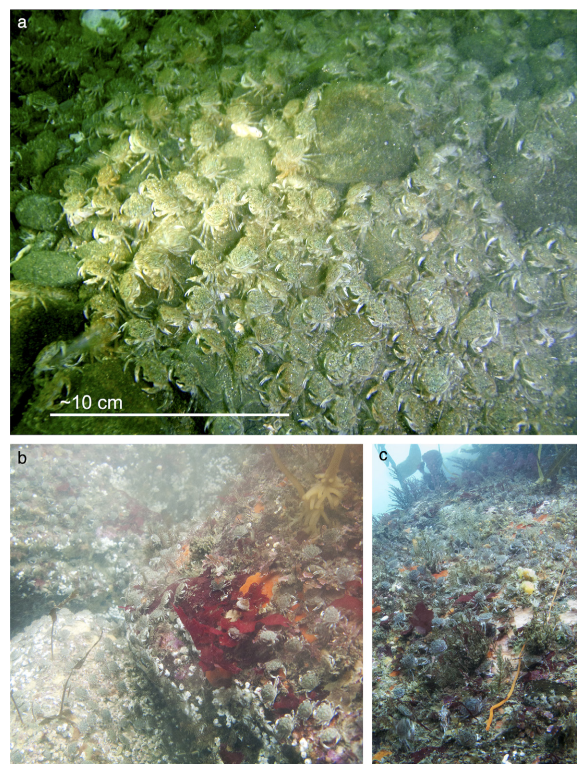

Fig. 1. (a) *Cancer magister* recruits on 13 May 2016, three weeks after the initial settlement at Graveyard Point, Port Orford, Oregon at ~13 m depth (Photo by A. Galloway). The picture was taken at an angle to the bottom making a determination of the image area difficult, but a reasonable estimate is between ~5000 and 11000 crabs/m^2 based on photo scaling derived from measured crab sizes. (b, c) Photos of newly settled crabs near the site in panel a, ~5 m depth, on 26 July 2008 (Photos by S. Groth). We could not calculate densities from these photos due to the angles, but present each to show the recruit aggregations in shallow rocky algal zones. Using large format versions, we counted n = 207 in panel b and n = 97 in panel c. Also see Appendix S2 for close-up, high-resolution versions of panel c.

~320–1,250 crabs/m^2. At locations with high recruit abundance, unusually large numbers of subadults and adults were also observed in shallow rocky habitats, perhaps cannibalizing smaller conspecifics. We have since learned from other biologists and divers in the region that recruitment events composed of hundreds of recruits per square meter (compared to tens of thousands per square meter in the exceptional event) have been observed along the West coast between 2005 and 2016. The day after his 19 April dive at Port Orford, Galloway observed high densities of new recruits in seagrass beds within Coos Bay (~85 km north). We know of other anecdotal observations of high-density aggregations in the intertidal (at least five occasions in Oregon estuaries, N. Terwilliger, *personal communication*), and subtidal in Washington (G. Jensen, *personal communication*), Oregon (S. Groth, *unpublished manuscript*; Fig. 1b, c; Appendix S2), and Northern California (Santa Cruz, K. Magana, *personal communication*). However, to our knowledge, such observations of *C. magister* have only been reported once in the literature (Shanks et al. 2010), and exceptionally high-density settlement events (e.g., >10,000 recruits/m^2) have not been described. It is plausible that exceptionally high-density recruitment events have simply gone unnoticed, as there is relatively little sport or research diving on the outer Pacific Coast between Bamfield, British Columbia, and Trinidad, Northern California (~675 km to north-northwest and ~275 km to south of Coos Bay, respectively).

To put these observations in context, 2016 was a particularly *low* year for megalopal abundance. For 16 years we have been monitoring the annual variation in *C. magister* larval success with daily sampling of megalopae using a light trap (Shanks 2013). The number of megalopae caught during the recruitment season (roughly April–September) has varied from a low of 2000 in the 1997 El Niño year to high catches in the millions during negative PDO years (Pacific Decadal Oscillation Index), a 1000-fold variation in megalopal abundance (Shanks 2013). In a 2007 ROV video taken off Cape Perpetua, Oregon (Video S2), recruit densities were as high as 439 crabs/m^2 and averaged 205 crabs/m^2 (Shanks et al. 2010). The year 2007 was a negative PDO year with very high catches of megalopae (1.7 million) and we hypothesized these high recruit densities were due to the huge numbers of megalopae that migrated to shore that year. However, although 2016 was a strong El Niño year, larval returns were very low, only slightly higher than in 1997. Dense aggregations of recruits have been observed in years with very high and also with very low returns of megalopae, suggesting the hypothesis that dense aggregations of new recruits may occur in many years. In the time series of annual megalopae return, daily catches of megalopae are pulsed, at ~2-week intervals (Roegner et al. 2007, Shanks 2013). If large settlement events occur on each pulse then there may be 10 to 12 large settlement events per season; it is presently unknown whether these regular larval pulses result in large, or exceptionally large settlement events.

C. magister megalopae are generally thought to settle into soft-sediment benthos in estuaries and a narrow, 15 km wide “coastal landing strip” (McConnaughey et al. 1994) and juvenile, age 0+ crab are generally expected to reside on sand and silt substrates (McConnaughey et al. 1992) where they are opportunistic, omnivorous consumers (Jensen and Asplen 1998) preying on soft sediment infauna (e.g., worms and small clams; Rasmuson 2013). During the initial observation on 19 April 2016 and during subsequent dives, it was clear that dense aggregations of new recruits were present on rocky and cobble substrates (Fig. 1; Video S3), and that these crabs were preying upon organisms on the bottom and even in the water column. For example, while filming individual crabs during a dive on 16 August 2016 at Port Orford, we documented possibly novel crab feeding behaviors; 0+ age recruits (mean = 11.6 mm, SD = 0.16, n = 88) were observed actively foraging on mysids swarming near the bottom (Video S3). Shortly after landing, recruits appear to aggregate into spatially explicit, higher-density “mobs.” Aggregation behavior has also been documented in other juvenile crabs (Efford 1965, Powell and Nickerson 1965). Grouping behaviors and patchy distributions were observed both by divers and on the ROV videos for both early settlers and age ~2+ juveniles (~8 cm carapace width; Appendix S3).

The ecological significance of recruitment events of this magnitude for crab population dynamics and energy flow through food webs are unknown, but potentially substantial and far reaching. (1) Extremely high-density crab settlements represent a nutritional subsidy (Polis et al. 1997) of energy and biomass from pelagic to nearshore food webs; for example, the biomass of ocean production in the form of new recruits transported to the coast in the first settlement event, was likely between 1 and 3 kg/m^2 (25 new recruits/g; A. L. Shanks, *unpublished data*). How does this energy subsidy from the open ocean move through nearshore food webs? Given that there may be multiple large settlement events during the recruitment season, do some members of the subtidal community depend on the seasonal influx of recruiting crabs? (2) Despite the economic and ecological importance of *C. magister*, surprisingly little is known about the process of recruitment of juvenile crabs. The initial recruitment of *C. magister* appears to occur, at least at times and perhaps normally, within dense aggregations. The dynamics of recruitment under these conditions have never been studied. At these densities, recruits would be vulnerable as both allospecific (e.g., particularly by fish) and conspecific prey, as recruits are highly cannibalistic (Fernandez 1999). (3) *C. magister* recruits are voracious and energetically demanding predators (Holsman et al. 2003, Rasmuson 2013). In dense aggregations, their feeding activities may be a form of episodic disturbance in shallow subtidal habitats, which has gone unobserved. How do extremely high-density recruitment events impact local nearshore communities? (4) The annual return of megalopae has varied by a factor of 1000 (Shanks 2013) and, in most years, large pulses of returning megalopae occur throughout the settlement season. During years with large numbers of returning megalopae, are aggregations of recruits even larger then we have observed? Does each pulse in returning megalopae generate dense aggregations of recruits? If so, then what is the effect of timing of arrival of settler cohorts on survival past the initial settlement stage? Are early arrivers at a competitive advantage or disadvantage relative to later settlers and how do different cohorts coexist (Pedersen and Guichard 2016)? Do cohorts consist of close relatives transported together through development, or do they represent a random sample from a well-mixed larval pool? (5) Finally, we know almost nothing about the spatial and temporal extent, or patchiness, of extremely high-density settlement events. The massive crab recruitment event documented here may have occurred along much of the southern Oregon Coast, separated by at least ~250 km, and recruits from this event persisted at high densities around Port Orford for at least five months. We do not know whether these observations were of a single, spatially contiguous landing. Exceptionally high-density recruitment events could be an important, but overlooked, biological force acting on *Cancer magister* populations and the ecology of nearshore coastal zones.

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Literature Cited

Literature citations are found in Appendix S1.

Aaron W. E. Galloway

Oregon Institute of Marine Biology, University of Oregon, PO Box 5389, Charleston, Oregon 97420 USA

E-mail: agallow3@uoregon.edu

Alan L. Shanks

Oregon Institute of Marine Biology, University of Oregon, PO Box 5389, Charleston, Oregon 97420 USA

Scott Groth

Oregon Department of Fish and Wildlife, P.O. Box 5003, Charleston, Oregon 97420 USA

Scott R. Marion

Oregon Department of Fish and Wildlife, Marine Resources Program, Newport, Oregon 97365 USA

Andrew R. Thurber

College of Earth, Ocean and Atmospheric Sciences, Oregon State University, Corvallis, Oregon 97331 USA

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Supporting Information

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