



## **Reproductive Potential Can Predict Recruitment Rates in Abalone**

Authors: Rossetto, Marisa, Leo, Giulio Alessandro De, Greenley, Ashley, Vazquez, Leo, Saenz-Arroyo, Andrea, et al.

Source: Journal of Shellfish Research, 32(1) : 161-169

Published By: National Shellfisheries Association

URL: <https://doi.org/10.2983/035.032.0122>

---

BioOne Complete ([complete.BioOne.org](https://complete.BioOne.org)) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](https://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

## REPRODUCTIVE POTENTIAL CAN PREDICT RECRUITMENT RATES IN ABALONE

MARISA ROSSETTO,<sup>1\*</sup> GIULIO ALESSANDRO DE LEO,<sup>1,2</sup> ASHLEY GREENLEY,<sup>2</sup>  
LEO VAZQUEZ,<sup>3</sup> ANDREA SAENZ-ARROYO,<sup>3</sup> JOSE ANTONIO ESPINOZA MONTES<sup>4</sup>  
AND FIORENZA MICHELI<sup>2</sup>

<sup>1</sup>Dipartimento di Scienze Ambientali, Università degli Studi di Parma, Parco Area delle Scienze 33A, I-43100 Parma, Italy; <sup>2</sup>Stanford University, Hopkins Marine Station, Pacific Grove, CA 93950;

<sup>3</sup>Comunidad y Biodiversidad A.C., Colonia Hipódromo Condesa, DF, México; <sup>4</sup>Sociedad Cooperativa de Producción Pesquera Buzos y Pescadores, Isla Natividad, Baja California Sur, México

**ABSTRACT** In many marine invertebrates, the relationship between egg production and/or number of competent larvae and subsequent recruitment is often unknown. Estimating such relationship is critical for informing the management and conservation of exploited species because it determines a natural population's response to exploitation. In the current study, recruitment rates of abalone *Haliotis fulgens* and *Haliotis corrugata* were recorded by means of postlarval collectors inside and outside 2 marine reserves in 2 subsequent years. At the same time and locations, theoretical reproductive outputs were computed by combining estimates of abalone densities and size structure with literature data on size-dependent fecundity and size at sexual maturity. We found that observed settlement rates correlated positively and significantly with estimated reproductive output, suggesting that greater production of eggs by large and fecund individuals can result in predictably high recruitment rates. In addition, the slope of the linear relationship suggests that the proportion of eggs that settle and metamorphose to become postlarvae is between 0.2% and 0.3%. Although affected by great uncertainty, this value constitutes a unique estimate of larval survival for the genus *Haliotis* in a natural environment.

**KEY WORDS:** larval survival, marine reserve, recruitment, sexual maturity

### INTRODUCTION

Establishing a stock–recruitment relationship (i.e., the relationship between parental stock size and subsequent recruitment) is a central problem of fish population dynamics, because stock–recruitment relationships regulate natural population size and determines its response to exploitation. Common models in population dynamics relating the recruitment  $R$  to spawner abundance  $N$  are the Beverton–Holt [ $R = aN/(1 + bN)$ ] (Beverton & Holt 1957) and the Ricker [ $R = aN \exp(-cN)$ ] models (Ricker 1954). The same functional forms can be used to relate the successful settlement to the number of eggs or of competent larvae. In these models, parameter  $a$  has dimensions of recruitment per spawner, or of settler per eggs, or settler per larvae (in the latter cases,  $a$  can be viewed as an index of survival), whereas parameters  $b$  and  $c$  are the density-dependent terms. Parameter  $a$  gives the slope of the functions at the origin and, regardless of which model is chosen, is a crucial variable in fishery population models; it determines the maximum reproductive rate, the vulnerability to recruitment overfishing, and the extinction probability, as well as the resilience, recovery time, and likely response to protection (Mace 1994, Myers & Mertz 1998, Botsford et al. 1999, Barrowman & Myers 2000).

Recruitment is recognized as one of the most variable features of the life cycle of many marine fishes and invertebrates, including the marine gastropod abalone (genus *Haliotis*) (McShane 1995, Rogers-Bennett et al. 2004, Miner et al. 2006). Within this genus, the existence of a stock–recruitment relationship linking new recruits to reproductive adult densities is a matter of continued debate (Shepherd 1990, Rogers-Bennett et al. 2004). Although the longest time series (17 y) of stock and recruitment data for abalone found no clear relationship between

adult populations and 2-y-old juveniles (Shepherd 1990), several studies show that greater adult densities support higher recruit abundance compared with depleted areas. An adult removal experiment by Prince et al. (1987) found a positive correlation between local adult density of *Haliotis rubra* and the number of newly settled individuals, suggesting that the relationship between recruits and reproductive individuals occurred at a local scale. Such localized effect in recruitment patterns is attributed to low larval dispersal distances documented in abalone, in the order of tens to hundred meters (Prince et al. 1987, McShane et al. 1988, Prince et al. 1988, Shepherd et al. 1992, Guzmán del Prío et al. 2000, Shanks et al. 2003, Micheli et al. 2012). Experimental studies by Rogers-Bennett et al. (2004) provided evidence that abundances of recruits for several Californian abalone species were significantly greater in Northern California, where abalone populations were found at relatively high densities, compared with sites in Southern California, where local populations were depleted. Recruitment failure was also found to be associated with low adult densities for black abalone *Haliotis cracherodii*, whereas higher adult population densities supported successful recruitment levels (Miner et al. 2006). Nevertheless, currently, no stock–recruitment relationship for the genus *Haliotis* has been proposed. Producing such a relationship is critical for demographic models for fishery management and for informing conservation strategies, such as the design of marine protected area networks and the possible translocation and aggregation of adults within depleted areas.

The goal of this study was to investigate the relationship between recruitment and reproductive potential for the green and pink abalone, *Haliotis fulgens* and *Haliotis corrugata*, using data from field surveys and recruitment experiments conducted in Isla Natividad, Baja California Sur, Mexico. In the fishing grounds surrounding the island, recruitment rates were quantified using larval collectors deployed on the seafloor inside and outside of 2 marine reserves created in 2006. In the same years

\*Corresponding author. E-mail: marisa.rossetto@nemo.unipr.it  
DOI: 10.2983/035.032.0122

and locations, the abundance and size structure of pink and green abalone were monitored yearly via scuba surveys. Last, detailed information on size-dependent fertility and size at sexual maturity for the 2 species was compiled from existing literature, allowing for estimates of the theoretical number of eggs produced by the abalone population. The analysis of these field and life history trait data sets allowed us to test whether estimated reproductive potential can predict recruitment rates in abalone and, if so, ultimately provide an estimate of abalone larval survival in a natural environment.

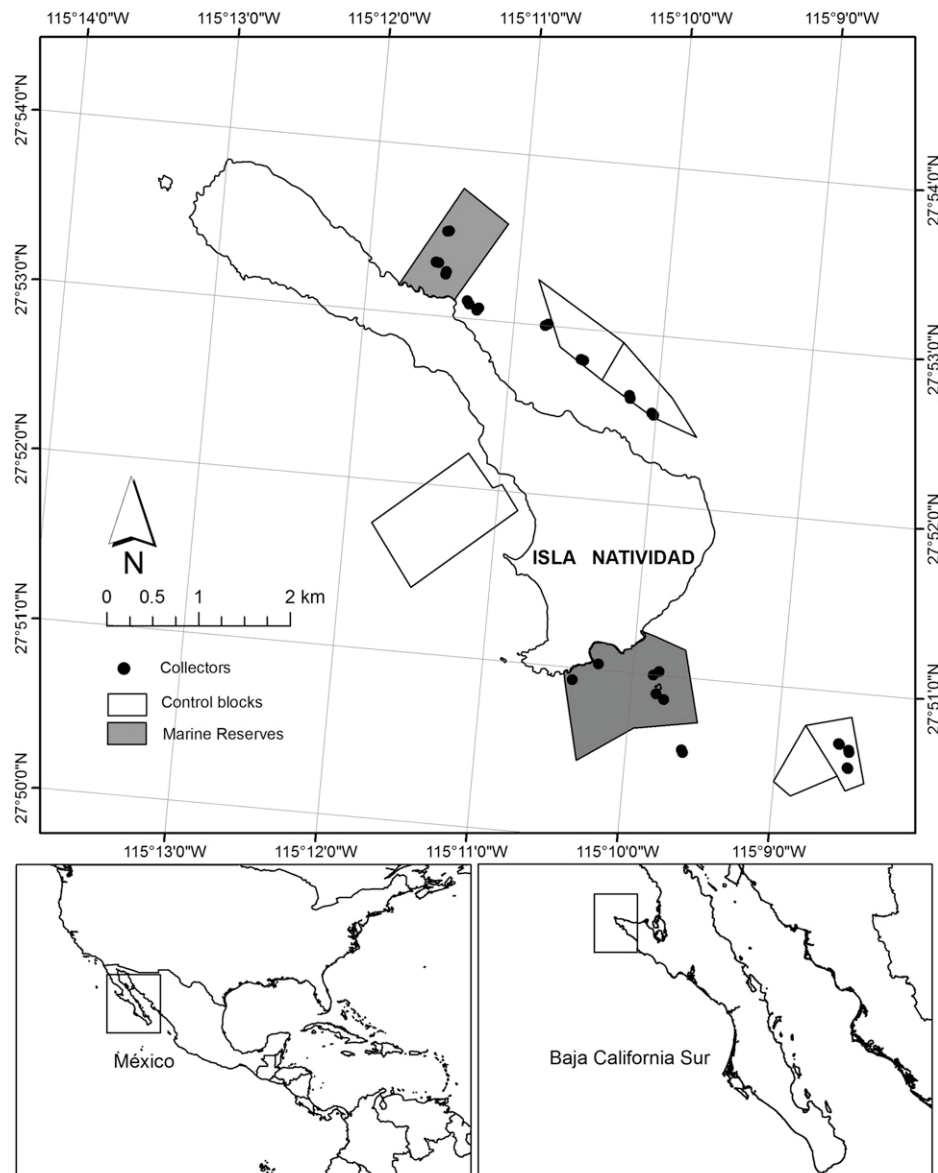
## MATERIALS AND METHODS

### Study Site

Isla Natividad is a small island off the Pacific coast of Baja California, Mexico (Fig. 1), with productive fishing grounds

induced by strong seasonal upwelling from approximately March until July. Around the island, nearshore waters are dominated by forests of the giant kelp *Macrocystis pyrifera* and rocky reefs that provide habitat for multiple species of abalone. The 2 most abundant species of abalone, green (*Haliotis fulgens*) and pink (*Haliotis corrugata*), occupy overlapping depth ranges of 0–15 m and 10–25 m, respectively.

In the Baja California region, abalone have been fished historically since the middle of the 19<sup>th</sup> century, first by Chinese fishermen (1860 to 1900) and Japanese divers (1900 to 1940), and, after 1940, by Mexican fishing cooperatives (Guzmán del Prío 1992). At Isla Natividad, the Mexican fishery for abalone started in 1956 (Shepherd et al. 1998). In 2006, the fishing cooperative at Isla Natividad established 2 no-take marine reserves—the Punta Prieta Reserve and the La Plana-Cueva Reserve—approximately 500 m and 1,000 m wide, respectively (Fig. 1). The reserves account for approximately 8% of the cooperative's fishing grounds



**Figure 1.** Location of Isla Natividad, Baja California Sur, Mexico. The 2 marine reserves and the fished reference sites are indicated. Black dots indicate sites where larval collectors were deployed.

and were established with the aim of recovering abalone populations and fishery yields.

### Data

Recruitment rates of pink and green abalone were monitored at Isla Natividad in 2008 and 2009 inside and outside 2 marine reserves (Fig. 1). Specifically, postlarval collectors measuring  $0.25 \times 0.25$  m were deployed underwater during the abalone spawning season (October to January) within the marine reserves at Punta Prieta ( $n = 8$  in 2008,  $n = 6$  in 2009) and La Plana-Cueva ( $n = 2$  in 2008,  $n = 6$  in 2009), and at 2 control fished sites—La Guanera ( $n = 8$  in 2008,  $n = 8$  in 2009) and La Dulce ( $n = 6$  in 2009; Fig. 1). The collectors were modified from designs published by Keesing et al. (1995) and Nash et al. (1995). Collectors were first deployed on November 20, 2008, followed by 3 subsequent plate exchanges on an approximately biweekly interval. Final retrieval of collector plates occurred on January 13, 2009. In 2009, the period of deployment was extended over the entire possible abalone's spawning season; collectors were first deployed on September 23 and plates were exchanged 4 times thereafter on an approximately biweekly interval. Final retrieval occurred on December 6, 2009. In the same years and locations, densities of pink and green abalone were monitored along replicate  $30 \times 2$ -m belt transects, whereas size frequencies (maximum shell length (SL), in centimeters) were measured during timed searches.

A detailed description of the field monitoring and recruitment studies conducted at Isla Natividad is reported in Micheli et al. (2012).

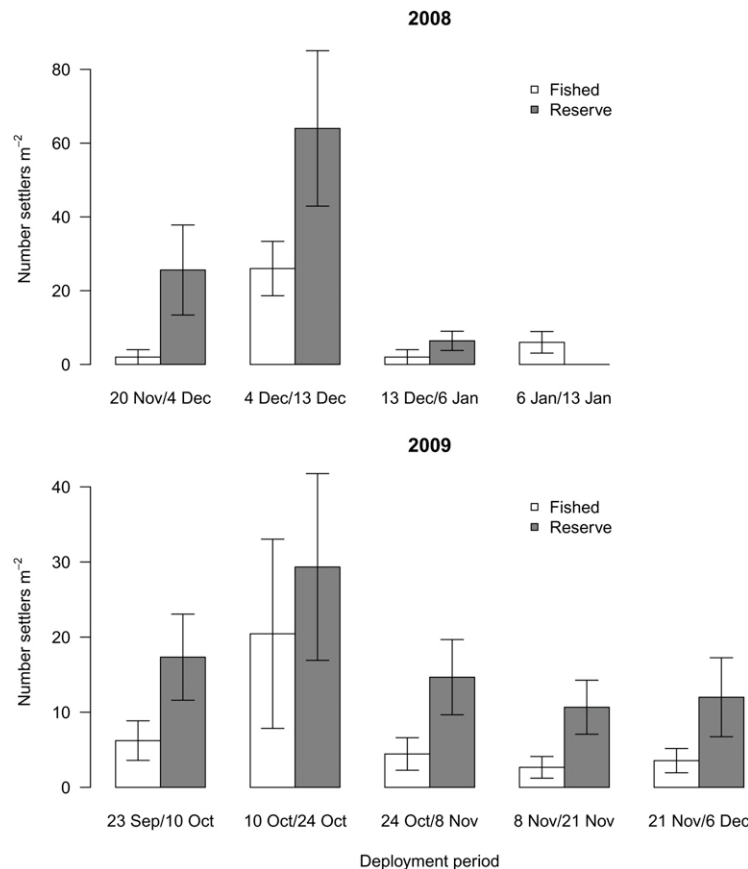
### Computation of Reproductive Output

Reproductive potential  $E$  was defined as the total number of abalone eggs produced per unit area. The reproductive potential depends on the density of mature abalone and, given that *Haliotis* fecundity increases with increasing body mass (Tutschulte 1976, Litaay & De Silva 2003), also on the size of individuals. A first estimate of *Haliotis corrugata* reproductive output in Isla Natividad has been reported by Micheli et al. (2012). Here, we refined the calculation of abalone egg production in Isla Natividad by including reproductive output of the other abalone species found on the island (i.e., *Haliotis fulgens*), fitting a sigmoid model of sexual maturity versus body size for both species, and accounting explicitly for the variability in eggs at unit weight.

Specifically, reproductive output in each year and location was calculated by summing the contribution of individuals of weight  $w$  using the following equation:

$$E = \sum_w 0.5 \xi_w \phi_w n_w \quad (1)$$

where 0.5 is the sex ratio (Tutschulte 1976),  $\xi_w$  is the fraction of sexually mature individuals of weight  $w$ ,  $\phi_w$  is the fecundity



**Figure 2.** Mean ( $\pm 1$  SE) number of abalone postlarvae (green and pink abalone cannot be distinguished morphologically at this early stage) on collectors deployed in reserves (Punta Prieta and La Plana) and in fished blocks (La Guanera and La Dulce), and collected after 2 wk on 4 dates between late November 2008 to mid January 2009 and between late September 2009 to early December 2009.

of individuals of size weight  $w$ , and  $n_w$  is the mean density (individuals per square meter) of individuals (estimated through the belt transects) of size  $w$ . Body weight  $w$  (in grams) was computed from individual shell length  $l$  (in millimeters) using the length–weight relationships reported in Shepherd et al. (1998):

$$w = 2.24 \times 10^{-5} l^{3.36} \text{ for } \textit{Haliotis fulgens}$$
$$w = 1.384 \times 10^{-5} l^{3.50} \text{ for } \textit{Haliotis corrugata}$$

To compute the fraction of sexually mature individuals  $\xi$ , we relied on the data in the study by Lluch-Belda et al. (1973) conducted in Baja California (Isla Cedros- Isla Natividad), that reported the percentage of sexually mature individuals of both green and pink abalone at different SLs. We fit the experimental data by performing a nonlinear least-square regression of an S-shaped curve, linking the fraction of sexually mature individuals  $\xi$  at length  $l$ :

$$\xi = \frac{1}{1 + \exp\left(-\frac{l - \eta}{\mu}\right)},$$

where  $l$  is the SL of individuals (in millimeters),  $\eta$  is the size at which 50% of individuals are sexually mature (in millimeters), and  $\mu$  is a parameter inversely proportional to the slope of the curve at  $l = \eta$ .

To estimate fecundities, the number of eggs  $e$  produced by a mature green abalone female was assumed to be a linear function of body mass (Tutschulte 1976, Litaay & De Silva 2003). For green abalone, egg production ranges from 2.56 million eggs at 180 mm in length to 3.45 million eggs at 174 mm in length (Tutschulte 1976). Assuming the length–weight relationship of Shepherd et al. (1998), this corresponds to a value of eggs per unit weight of between 3,015–4,530 eggs/g. For pink abalone, the number of eggs produced by a mature female ranges from 1.25 million eggs at a length of 159 mm to 2.32 million eggs at a length of 162 mm (Tutschulte 1976), which corresponds to a value of eggs per unit weight of between 1,386–3,088 eggs/g (Shepherd et al. 1998). It follows that  $\phi_w = ew$ , with  $e$  varying from 3,015–4,530 for *Haliotis fulgens* and from 1,368–3,088 for *Haliotis corrugata*.

For both species, we calculated the reproductive output for green and pink abalone in 2008 and 2009 at each location, and by combining locations in protected and unprotected areas. To obtain a range of variation associated with the estimated reproductive output, we performed 10,000 simulations in which, at each replication, we bootstrapped the size–frequency distributions and density estimates, and randomly sampled the value of egg production  $e$  over the range of variation reported for the 2 species. The mean and SE of the reproductive output were computed on the 10,000 bootstrap replicates. Given that the recruitment experiment did not discriminate between species (recruits are too small to distinguish between green and pink abalone), we calculated the total reproductive output by summing the contribution of pink and green reproductive outputs. The standard bootstrapped error of the total reproductive output was calculated on the basis of the error propagation theory (i.e., as the square root of the sum of the squared errors of green and pink reproductive outputs).

TABLE I.  
Cumulative abalone recruitment rates summed over the entire collector deployment period and green and pink abalone densities (from scuba diving surveys) in 2008 and 2009 in the monitoring sites separately and combined, and in the fished and reserve areas.

Site	Settler density (no./m <sup>2</sup> ), mean (SD)		Abalone density (no./m <sup>2</sup> ), mean (SD)			
	<i>Haliotis fulgens</i> + <i>Haliotis corrugata</i>		<i>H. fulgens</i>		<i>H. corrugata</i>	
	2008	2009	2008	2009	2008	2009
La Dulce	—	32 (20.23), $n = 6$	0.0156 (0.0268), $n = 16$	0.0067 (0.0160), $n = 25$	0.0323 (0.0392), $n = 16$	0.0093 (0.0199), $n = 25$
La Guanera	36 (23.81), $n = 8$	20 (22.22), $n = 8$	0.0119 (0.0259), $n = 21$	0.0058 (0.0171), $n = 23$	0.0317 (0.0505), $n = 21$	0.0167 (0.0195), $n = 23$
Fished sites combined	36 (23.81), $n = 8$	25.14 (21.48), $n = 14$	0.0135 (0.0260), $n = 37$	0.0062 (0.0164), $n = 48$	0.0320 (0.0454), $n = 37$	0.0128 (0.0198), $n = 48$
La Plana-Cueva	152 (33.94), $n = 2$	58.7 (38.76), $n = 6$	0.0175 (0.0321), $n = 19$	0.0282 (0.0421), $n = 26$	0.0254 (0.0374), $n = 19$	0.0218 (0.0257), $n = 26$
Punta Prieta	82 (77.65), $n = 8$	109.3 (52.01), $n = 6$	0.0144 (0.0232), $n = 22$	0.0021 (0.0056), $n = 24$	0.0432 (0.0534), $n = 22$	0.0194 (0.0195), $n = 24$
Reserve sites combined	96 (75.42), $n = 10$	84 (51.11), $n = 12$	0.0159 (0.0274), $n = 41$	0.0157 (0.0331), $n = 50$	0.0350 (0.0470), $n = 41$	0.0207 (0.0227), $n = 50$



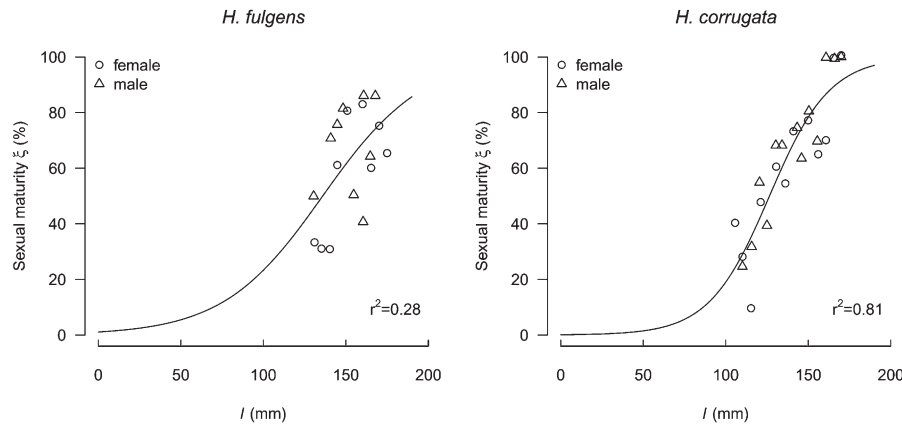


Figure 3. Fraction  $\xi$  of sexually mature individuals of *Haliotis fulgens* and *Haliotis corrugata* as a function of individual length ( $l$ ). Circles are data obtained from Lluch-Belda et al. (1973); the solid line represents the fitted sigmoid curve.

#### Relationship Between Settlement and Reproductive Output

A common assumption made for marine invertebrates is that the number of successful settlers depends on the availability of competent larvae (Botsford et al. 1999). For abalone, as for other marine broadcast spawners, available habitat for settlement can be a limiting factor when larvae are at high densities (McShane 1992, Shepherd 1973, Botsford et al. 1999, Sladek-Nowlis & Roberts 1999). Assuming that the number of larvae is simply equal to the number of eggs  $E$  multiplied for fertilization success, we can use a Beverton-Holt or Ricker model to describe the dependence of successful settlers  $S$  on the total number of eggs  $E$  as follows:

$$S = \frac{aE}{1 + bE} \quad (2)$$

or

$$S = aE \exp(-cE) \quad (3)$$

where parameter  $a$  represents the maximum survival from egg to settlers, and parameters  $b$  and  $c$  represent the strength of density dependence in the 2 model formulations.

In Isla Natividad, however, where abalone populations are highly depleted (Shepherd et al. 1998, Micheli et al. 2012), it is unlikely that density dependence occurs. Therefore, we can assume that the number of settlers is simply proportional to the number of eggs:

$$S \approx aE \quad (4)$$

To estimate the value of  $a$ , we performed a least-square linear regression between the observed settlement (summed over the entire period of collector deployment) and the estimated total reproductive output setting the value of intercept equal to 0. Regression through the origin is reasonable because 0 egg production would correspond to 0 settlement, which is considered adequate if the intercept of the ordinary linear regression is not significantly different from 0 (Eisenhauer 2003).

To take into account the uncertainty in the predicted and explanatory variables explicitly, we replicated the linear regression estimation on 1,000 bootstrapped samples of reproductive output and settlement rates. We then calculated the mean and

the 95% confidence interval (CI) of the 1,000 obtained slopes, and computed how many times they were significant at the 0.05 level.

#### RESULTS

Abalone recruitment rates on collectors varied among the deployment periods (Fig. 2). The maximum recruitment abundance during a 2-wk deployment was 176 settlers/m<sup>2</sup>. Cumulative recruitment rates, summed over the entire deployment period, varied from 20–152 settlers/m<sup>2</sup> (Table 1). As reported by Micheli et al. (2012), both in 2008 and 2009, recruitment rates registered in the protected sites were significantly greater relative to the unprotected areas during all deployment periods (Fig. 2).

The survey of abalone abundance at Isla Natividad revealed densities of individuals consistently less than 0.05 individuals/m<sup>2</sup> (Table 1). Green abalone densities ranged from 0.002–0.017 individual/m<sup>2</sup>, whereas pink abalone densities were relatively higher, ranging from 0.009–0.043 individual/m<sup>2</sup>. As reported by Micheli et al. (2012), densities of both species were similar inside and outside protected areas (i.e., there was no significant effect of protection on abalone abundance). Instead, in 2009, pink abalone showed a significant reduction in densities relative to 2008 as a result of a mortality event in summer and spring 2009 (Micheli et al. 2012).

TABLE 2.

Parameter of the S-shaped curve describing the percentage of sexually mature individuals as a function of shell length fitted on the experimental data from Lluch-Belda et al. (1973) for green and pink abalone.

Parameter	Estimate	SE	<i>t</i> value	<i>P</i> value	2.5%	97.5%
<i>Haliotis fulgens</i>						
$\eta$	135.99	7.77	17.50	7.43e – 12*	43.05	147.28
$\mu$	30.20	12.43	2.43	0.0273†	15.82	230.35
<i>Haliotis corrugata</i>						
$\eta$	126.50	2.27	55.64	<2e – 16*	121.36	131.02
$\mu$	18.29	2.54	7.21	2.44e – 07*	13.87	24.57

\* Significant at 0.01 level.

† Significant at 0.05 level.

The fraction of mature individuals as a function of length for *Haliotis fulgens* and *Haliotis corrugata* is depicted in Figure 3, along with the sigmoid curves fitted to the data. Estimated parameters were significant in both cases (Table 2). The models indicate that the size at sexual maturity (i.e., the size at which 50% of individuals are sexually mature) occurs at an SL of  $136 \pm 7.8$  mm for green abalone and at an SL of  $126.5 \pm 2.3$  mm for pink abalone.

The size–frequency distributions of both species showed a greater abundance of large individuals inside protected areas relative to fished sites (Fig. 4). In particular, the percentage of sexually mature individuals, although variable among sites (Table 3), was always greater inside marine reserves relative to unprotected areas (Table 3, Fig. 4), indicating that protection from fishing ensured a high presence of reproductive individuals among the population.

Estimated reproductive output ranged from 1,797–25,856 eggs/m<sup>2</sup> for *Haliotis fulgens* and from 3,792–17,931 eggs/m<sup>2</sup> for *Haliotis corrugata*. The variation in the estimated reproductive output reflects the variation in densities and in the size–frequency distributions. Despite the high variability, estimated reproductive output was always greater in the protected areas (within reserves) than in the unprotected areas (Table 3). Estimated reproductive output was between 1.4 and 3 times greater inside the reserve than outside for *H. fulgens*, and about 2 times higher for *H. corrugata* (Table 3).

Settlement rates correlated positively with estimated reproductive outputs, suggesting that greater egg production supports greater larval settlement (Table 4, Fig. 5). The relationship between settlement and estimated reproductive output showed substantial variation when performed on the monitoring sites separately (Fig. 5A; slope =  $2.41 \times 10^{-3}$ ; 95%

CI,  $1.92 \times 10^{-3}$ – $2.96 \times 10^{-3}$ ), whereas lower variation and an improvement in the significance level of the slope was observed when combining data from different sites (Fig. 5B; slope =  $3.09 \times 10^{-3}$ ; 95% CI,  $2.35 \times 10^{-3}$ – $3.93 \times 10^{-3}$ ). The estimated slopes, not significantly different from each other (Table 4), indicate that, in a natural environment, around 0.2–0.3% of abalone eggs released in the water column are fertilized and metamorphose to postlarvae.

## DISCUSSION

Estimating stock–recruitment relationships is critical for informing the management and conservation of exploited species. However, data scarcity and high variability in recruitment often make this task challenging. Here, we found that reproductive output could be a good predictor of recruitment rates of an exploited, valuable marine invertebrate. This finding confirms previous indications that, although abalone recruitment can be highly variable, high densities of large, fecund individuals can support relatively high recruitment rates. In addition, the estimated slope ( $\sim 2\text{--}3 \times 10^{-3}$ ) provides an estimate of the proportion of eggs that settle and metamorphose to become postlarvae. Our computation assumes that all the eggs are released during the spawning period, and that the collector deployment period fully encompasses the entire reproductive season so that the total number of settlers observed during the experiment effectively represents the actual yearly recruitment of abalone. Although affected by great uncertainty, this value constitutes, to our knowledge, the only available estimate of abalone larval survival in a natural environment. In general, estimates of larval survival are extremely rare and difficult to obtain in the marine environment. So far, only indirect and speculative guesses had been made

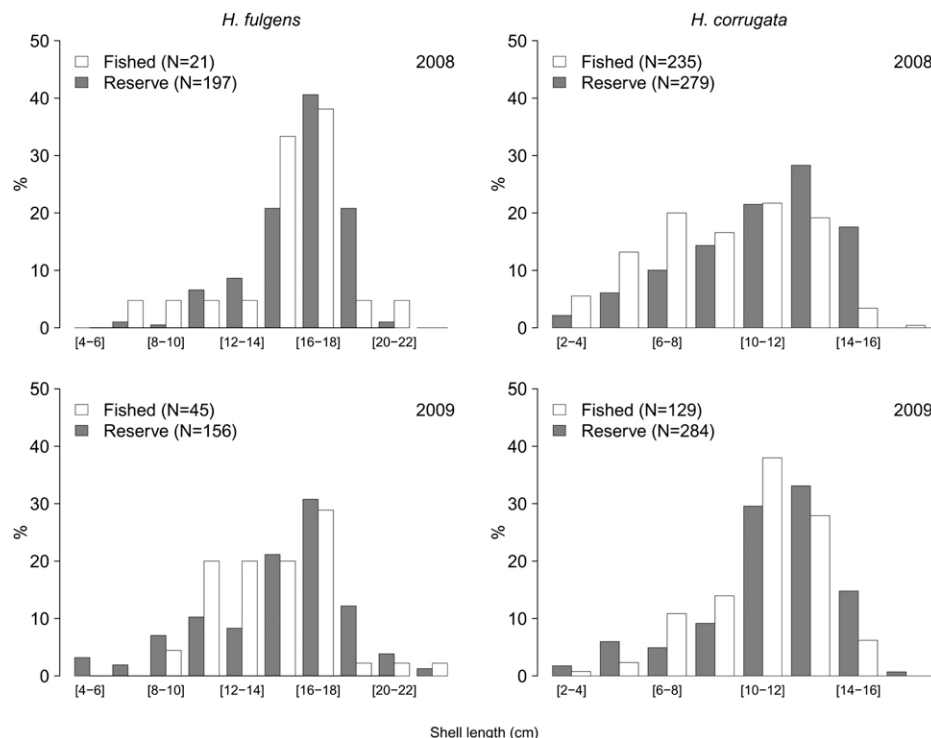


Figure 4. Size–frequency distribution of *Haliotis corrugata* and *Haliotis fulgens* inside and outside the marine reserves of Isla Natividad in 2008 and 2009.

TABLE 3.

Percentage of individuals above size at sexual maturity and estimated reproductive output for green and pink abalone in 2008 and 2009 in the monitoring sites separately and in the fished and reserve areas combined.

	Individuals above size at sexual maturity (%)		Estimated reproductive output (eggs/m <sup>2</sup> )*	
	2008	2009	2008	2009
<i>H. fulgens</i>				
La Dulce	84.6 (n = 13)	70.7 (n = 41)	12,948 (6,023)	5,078 (2,599)
La Guanera	87.5 (n = 8)	75 (n = 4)	10,979 (6,319)	3,334 (2,502)
Fished sites combined	85.7 (n = 21)	71.1 (n = 45)	11,585 (4,319)	4,649 (1,947)
La Plana-Cueva	92.2 (n = 141)	72 (n = 132)	18,568 (7,908)	25,856 (8,232)
Punta Prieta	78.6 (n = 56)	79.2 (n = 24)	14,217 (5,271)	1,797 (1,031)
Reserve sites combined	88.3 (n = 197)	73.1 (n = 156)	16,412 (4,791)	14,309 (4,705)
<i>H. corrugata</i>				
La Dulce	48.7 (n = 117)	82.1 (n = 39)	6,860 (2,638)	3,792 (1,893)
La Guanera	40.7 (n = 118)	67.8 (n = 90)	6,960 (3,031)	4,687 (1,582)
Fished sites combined	44.7 (n = 235)	72.1 (n = 129)	6,883 (2,265)	4,135 (1,324)
La Plana-Cueva	73.5 (n = 34)	82.3 (n = 153)	9,161 (3,830)	10,388 (3,373)
Punta Prieta	66.5 (n = 245)	73.3 (n = 131)	17,931 (6,176)	6,705 (2,073)
Reserve sites combined	67.4 (n = 279)	78.2 (n = 284)	14,282 (4,491)	8,560 (2,370)

\* Mean values of reproductive output are reported; bootstrapped standard errors are reported in brackets.

for abalone. Interestingly, these previous numbers are of similar magnitude as our estimate. In particular, Rogers-Bennett and Leaf (2006) indicated, for a population at stable equilibrium (i.e., neither growing nor decreasing), a first-year survival (representing fertilization success, survival in the larval stage, and early postsettlement survival during the first year) of  $2.13 \times 10^{-5}$  and  $1.35 \times 10^{-6}$  for red and white abalone, respectively (note that these figures also account for survival during the first year—that is, an SL up to 25 mm and 35 mm, respectively). Bardos et al. (2006), when constructing a matrix model for *Haliotis rubra*, assumed a fertilization success of 0.47 and an order of magnitude of  $10^{-3}$  for the proportion of fertilized eggs that survive up to postlarvae, suggesting a value of  $a = 4.7 \times 10^{-4}$ . Our estimates of abalone larval survival are also comparable with values reported for other marine invertebrates. For red sea urchin, Botsford et al. (1999) suggested values of survival from competent larvae to settlement between  $2 \times 10^{-3}$  and  $2 \times 10^{-4}$ , with the most probable values between  $2 \times 10^{-3}$  and  $4 \times 10^{-3}$ . These figures would suggest that, in the marine environment, only a very small fraction of eggs eventually become postlarvae.

Densities of abalone recorded in Isla Natividad show that the populations are highly depleted, well below the value at which recruitment failure is expected to occur (i.e., 0.2–0.3 individuals/m<sup>2</sup>) (Babcock & Keesing 1999). Nevertheless, recruitment was detected in all protected and fished sites, with higher recruitment levels observed inside protected areas (despite similar abalone densities). Recruitment rates registered at Isla Natividad were similar to those registered in previous recruitment experiments on several species of abalone conducted using artificial collectors. Recruitment rates varied from 30–90 settlers/m<sup>2</sup> over periods of 2 wk and 1 mo for *Haliotis iris* (Aguirre & McNaught 2011), peaks of 45–114 settlers/m<sup>2</sup> were observed for *Haliotis rubra* and *Haliotis laevigata* by Nash (1992), and peaks up to 2,347 postlarvae/m<sup>2</sup> were registered for *H. rubra* by Nash et al. (1995).

The size at sexual maturity estimated in the current study for the 2 abalone species is comparable with previous estimations

made in the area. Guzmán del Prío (1992) suggest that the size at sexual maturity is an SL of 138 mm for *Haliotis corrugata* and an SL of 152 mm for *Haliotis fulgens*, whereas Shepherd et al. (1998) suggest much lower estimates in SL, 103.5 mm and 121.5 mm, respectively. Our analysis provided intermediate figures for both species.

In our analysis, the correlation between reproductive output and settlement rate was highly variable, especially at a very local scale. This could be a result of the patchy distribution of abalone populations, the heterogeneity in habitat condition and community composition, and/or variability in ecological interaction strength, such as competition and presence of predators. The relationship between recruitment and egg production is also likely to be influenced strongly by oceanographic factors such as currents and storms, which could potentially limit recruitment when egg production is elevated.

Our study shows that estimates of reproductive output in abalone can serve as an indicator of recruitment rates, at least within the density range observed in the study site. Such information is extremely valuable for demographic models used in abalone fishery conservation and management. It is likely that the linearity between these 2 variables does not hold at lower and higher egg production because of both positive and

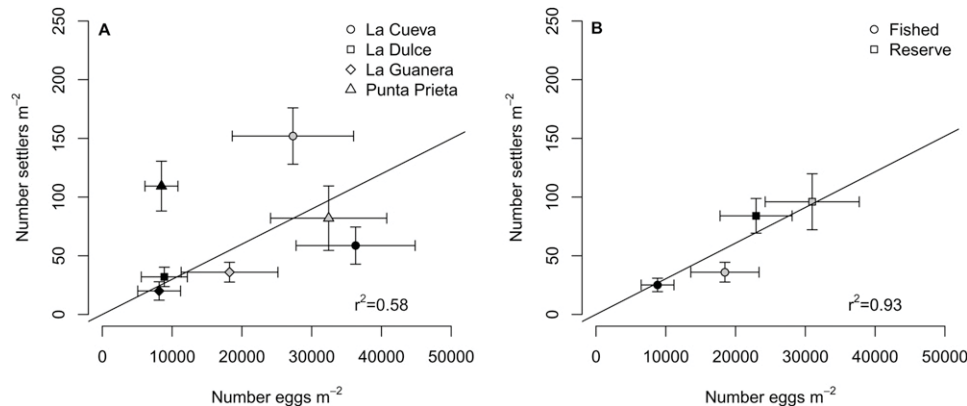
TABLE 4.

Linear regression of observed settlement rate versus estimated reproductive output (computed setting the intercept equal to 0) on the monitoring sites separately and combined in fished and protected zones.

Estimate	P value	2.5%	97.5%	r <sup>2</sup>
Monitoring sites separately (n = 7)				
$2.41 \times 10^{-3}$	0.12	$1.92 \times 10^{-3}$	$2.96 \times 10^{-3}$	0.58
Fished and reserve sites combined (n = 4)				
$3.09 \times 10^{-3}$	0.006*	$2.35 \times 10^{-3}$	$3.93 \times 10^{-3}$	0.93

\* Significant at the 0.01 level.





**Figure 5. (A, B) Relationship between the observed settlement rate (cumulative number of larvae per square meter  $\pm$  SE) and the estimated egg production (mean  $\pm$  bootstrapped SE) for green and pink abalone combined in 2008 (gray symbols) and 2009 (black symbols) for the 4 locations separately (A) and grouped in protected and unprotected zones (B). The slope of the linear model with a 0 intercept represents parameter  $a$ , maximum egg survival in conditions of low densities.**

negative density-dependent processes. Indeed, at very low egg densities, fertilization could be impaired, whereas at high larval densities, suitable habitat for settlement could be a limiting factor. Analyzing the relationship between egg production and settlement rates over broader ranges in egg densities would provide clues regarding at what levels density dependence may act as well as provide a better understanding the shape of stock–recruitment relationships for these 2 species.

#### ACKNOWLEDGMENTS

We thank the fishermen of the cooperative Buzos y Pescadores of Isla Natividad for their collaboration and support. This work was supported through funds from the Walton Family Foundation and from the Italian Ministry of Research (PRIN project 2008 and Interlink project no. II04CE49G8). This work has been supported also by funds from the NSF Coupled Natural Human Systems.

#### LITERATURE CITED

- Aguirre, J. D. & D. C. McNaught. 2011. Habitat modification affects recruitment of abalone in central New Zealand. *Mar. Biol.* 158:505–513.
- Babcock, R. & J. Keesing. 1999. Fertilization biology of the abalone *Haliotis laevis*: laboratory and field studies. *Can. J. Fish. Aquat. Sci.* 56:1668–1678.
- Bardos, D. C., R. W. Day, N. T. Lawson & N. A. Linacre. 2006. Dynamical response to fishing varies with compensatory mechanism: an abalone population model. *Ecol. Modell.* 192:523–542.
- Barrowman, N. J. & R. A. Myers. 2000. Still more spawner–recruitment curves: the hockey stick and its generalizations. *Can. J. Fish. Aquat. Sci.* 57:665–676.
- Beverton, R. J. H. & S. J. Holt. 1957. On the dynamics of exploited fish populations. London: Chapman and Hall. 533 pp.
- Botsford, L. W., L. E. Morgan, D. L. Lockwood & J. E. Wilen. 1999. Marine reserves and management of the Northern California red sea urchin fishery. *Calif. Coop. Ocean. Fish. Investig. Rep.* 40:87–93.
- Eisenhauer, J. G. 2003. Regression through the origin. *Teach. Stat.* 25: 76–80.
- Guzmán del Prío, S. A. 1992. A review of the biology of abalone and its fishery in Mexico. In: S. A. Shepherd, M. J. Tegner & S. A. Guzmán del Prío (ed.). *Abalone of the world: biology, fisheries and culture*. Blackwells, Oxford, U. pp. 341–360.
- Guzmán del Prío, S. A., F. Salinas, O. Zaytsev, J. Belmar-Pérez & J. Carrillo-Laguna. 2000. Potential dispersion of reproductive products and larval stages of abalone (*Haliotis* spp.) as a function of the hydrodynamics of Bahía Tortugas, Mexico. *J. Shellfish Res.* 19:869–881.
- Keesing, J. K., R. Grovejones & P. Tagg. 1995. Measuring settlement intensity of abalone: results of a pilot-study. *Mar. Freshw. Res.* 46:539–543.
- Litaay, M. & S. S. De Silva. 2003. Spawning season, fecundity and proximate composition of the gonads of wild-caught blacklip abalone (*Haliotis rubra*) from Port Fairy waters, southeastern Australia. *Aquat. Living Resour.* 16:353–361.
- Lluch-Belda, D., S. A. Guzmán del Prío, V. Marín Aceves & M. Ortíz Quintanilla. 1973. La pesquería de abulón en Baja California: un análisis de su desarrollo y perspectivas futuras. Mexico: Instituto Nacional de la Pesca. *Ser. Información* 6:1–21.
- Mace, P. M. 1994. Relationships between common biological reference points used as thresholds and targets of fisheries management strategies. *Can. J. Fish. Aquat. Sci.* 51:110–122.
- McShane, P. E. 1992. Early life of abalone: a review. In: S. A. Shepherd, M. J. Tegner & S. A. Guzmán del Prío, editors. *Abalone of the world: biology, fisheries and culture*. Oxford: Blackwell. pp. 120–140.
- McShane, P. E. 1995. Recruitment variation in abalone: its importance to fisheries management. *Mar. Freshw. Res.* 46:555–570.
- McShane, P. E., K. P. Black & M. G. Smith. 1988. Recruitment processes in *Haliotis rubra* (Mollusca: Gastropoda) and regional hydrodynamics in southeastern Australia imply localized dispersal of larvae. *J. Exp. Mar. Biol. Ecol.* 124:175–203.
- Micheli, F., A. Saenz-Arroyo, A. Greenley, L. Vazquez, J. A. Espinoza Montes, M. Rossetto & G. A. De Leo. 2012. Marine reserves enhance population resilience to climatic impacts. *PLoS ONE* 7:e40832.
- Miner, C. M., J. M. Altstatt, P. T. Raimondi & T. E. Minchinton. 2006. Recruitment failure and shifts on community structure following mass mortality limit recovery prospects of black abalone. *Mar. Ecol. Prog. Ser.* 327:107–117.
- Myers, R. A. & G. Mertz. 1998. The limits of exploitation: a precautionary approach. *Ecol. Appl.* 8:165–169.
- Nash, W. J. 1992. What do abalone spat settlement studies measure? The influence of substrate attractiveness on abalone larval settlement rate to artificial surfaces. In: D. A. Hancock, editor. *Recruitment processes*. Australian Society for Fish Biology Workshop, Hobart, 21

- August 1991. Bureau of Rural Resources proceedings no. 16. Canberra: Australian Government Publishing Service. pp. 26–31.
- Nash, W. J., J. C. Sanderson, J. Bridley, S. Dickson & B. Hislop. 1995. Post-larval recruitment of blacklip abalone (*Haliotis rubra*) on artificial collectors in southern Tasmania. *Mar. Freshw. Res.* 46:531–538.
- Prince, J. D., T. L. Sellers, W. B. Ford & S. R. Talbot. 1987. Experimental evidence for limited dispersal of haliotid larvae (genus *Haliotis*; Mollusca: Gastropoda). *J. Exp. Mar. Biol. Ecol.* 106:243–263.
- Prince, J. D., T. L. Sellers, W. B. Ford & S. R. Talbot. 1988. Confirmation of relationship between the localized abundance of breeding stock and recruitment for *Haliotis rubra* Leach (Mollusca: Gastropoda). *J. Exp. Mar. Biol. Ecol.* 122:91–104.
- Ricker, W. E. 1954. Stock and recruitment. *J. Fish. Res. Board Can.* 11:559–623.
- Rogers-Bennett, L., B. L. Allen & G. E. Davis. 2004. Measuring abalone (*Haliotis* spp.) recruitment in California to examine recruitment overfishing and recovery criteria. *J. Shellfish Res.* 23:1201–1207.
- Rogers-Bennett, L. & R. T. Leaf. 2006. Elasticity analyses of size-based red and white abalone matrix models: management and conservation. *Ecol. Appl.* 16:213–224.
- Shanks, A., B. A. Grantham & M. H. Carr. 2003. Propagule dispersal distance and the size and spacing of marine reserves. *Ecol. Appl.* 13:S159–S169.
- Shepherd, S. A. 1973. Studies on Southern Australian abalone (Genus *Haliotis*): 1. Ecology of five sympatric species. *Aust. J. Mar. Freshw. Res.* 24:217–257.
- Shepherd, S. A. 1990. Studies on Southern Australian abalone (genus *Haliotis*): long-term recruitment and mortality dynamics of an unfished population. *Aust. J. Mar. Freshw. Res.* 41:475–492.
- Shepherd, S. A., D. Lowe & D. Partington. 1992. Studies on Southern Australian abalone (genus *Haliotis*) XIII: larval dispersal and recruitment. *J. Exp. Mar. Biol. Ecol.* 164:247–260.
- Shepherd, S. A., J. R. Turrubiates-Morales & K. Hall. 1998. Decline of the abalone fishery at la Natividad: overfishing or climate change? *J. Shellfish Res.* 17:839–846.
- Sladek-Nowlis, J. & C. M. Roberts. 1999. Fisheries benefits and optimal design of marine reserves. *Fish Bull.* 97:604–616.
- Tutschulte, T. C. 1976. The comparative ecology of three sympatric abalone. PhD diss., University of California at San Diego.