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Fishery management priorities vary with self-recruitment in sedentary marine populations

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Abstract. Fisheries science often uses population models that assume no external recruitment, but nearshore marine populations harvested on small scales of <200 km often exhibit an unknown mix of self-recruitment and recruitment from external sources. Since empirical determination of self-recruitment vs. external recruitment is difficult, we used a modeling approach to examine the sensitivity of fishery management priorities to recruitment assumptions (self [closed], external [open]) in a local population of harvested giant clams (*Tridacna maxima*) on Mo'orea, French Polynesia. From 2006 to 2010, we measured growth, fecundity, recruitment, and survival (resulting from natural and fishing mortality). We used these data to parameterize both a closed (complete self-recruitment) and an open (no self-recruitment) integral projection model (IPM), and then calculated elasticities of demographic rates (growth, survival, recruitment) to future population abundance in 20 years. The models' lowest projected abundance was 93.4% (95% CI, [86.5%, 101.8%]) of present abundance, if the local population is entirely open and the present level of fishing mortality persists. The population will exhibit self-sustaining dynamics ($1 \leq \lambda \leq 1.07$) as for a closed population if the ratio of self-recruits per gram of dry gonad is >0.775 (equivalent to 52.85% self-recruitment under present conditions). Elasticity analysis of demographic parameters indicated that future abundance can most effectively be influenced by increasing survival of mid-sized clams (~80–120 mm) if the population is self-sustaining, and by increasing survival of juvenile clams (~40–70 mm) if the population is non-self-sustaining (as for an open population). Our results illustrate that management priorities can vary depending on the amount of self-recruitment in a local population.

Key words: closed population; coral reef fishery; fishing mortality; giant clam; integral projection model; local population; mixed recruitment; Mo'orea, French Polynesia; open population; self-recruitment; small-scale fishery; *Tridacna*.

INTRODUCTION

The degree to which a local marine population is closed and self-recruiting, vs. open and supplied by recruitment from external populations, is scale dependent and can drive population dynamics (Gaines and Bertness 1992, Underwood and Keough 2001, Armsworth 2002). Local populations in marine systems were long considered to be functionally open (Caley et al. 1996), but are now widely recognized as a mix of open and closed at the scale of reefs or islands (Mora and Sale 2002, Sponaugle et al. 2002, Swearer et al. 2002, Jones et al. 2009). However, logistical challenges have resulted in only a few studies that have empirically estimated the proportion of total recruitment attributed to self-recruitment in a local population, which can generally

range from ~5% to 80% of total recruitment (Almany et al. 2007, Carreras-Carbonell et al. 2007, Jones et al. 2009, Christie et al. 2010). Understanding local population dynamics and the role of recruitment is of great interest to ecologists, but is also fundamental for the effective management of many marine species, as in the case of establishing marine reserves (Gerber et al. 2003, Sale et al. 2005) and managing fisheries (Cushing 1995).

The amount of self-recruitment relative to external recruitment in a local population can determine whether that population exhibits dynamics similar to a closed population vs. an open population (Armsworth 2002). Closed populations in their simplest form exhibit geometric (exponential) growth, especially over short time scales starting from initial low abundances (Gurney and Nisbet 1998, Gotelli 2008), but can be regulated by several density-dependent processes including density-dependent growth, mortality, and reproduction (Murdoch 1994, Turchin 1995, Hixon et al. 2002). If the external recruit supply is constant, then open populations can be regulated in the absence of local density dependence because the per capita recruitment rate changes as a function of adult abundance (Caley et al.

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1996); this is known as “recruitment regulation” (Hughes 1990).

Many models originally developed for management of commercial fisheries at large spatial scales consider recruitment in a population to be fully closed instead of mixed, but these closed models do not accurately describe the potential dynamics of local populations at smaller spatial scales (Hilborn et al. 2005, Orensanz et al. 2005). This misrepresentation stems from the inclusion of an assumed stock-recruitment relationship without external recruitment in most fisheries models (Hilborn and Walters 1992, Walters and Martell 2004). However, the connectivity between stock and subsequent recruitment for local populations can be intermittent and heterogeneous on annual time scales, due mainly to stochastic patterns in nearshore water circulation, but also the pulse nature of larval transport (Siegel et al. 2008). These processes result in spatially structured metapopulations of local populations that are typically unmanageable using conventional stock-recruitment relationships (Orensanz et al. 2005), yet they are often managed at the local population scale with closed population models that assume just such a relationship (Medley et al. 1993). When such local populations are managed as a single closed population, high uncertainty in management is generated, especially in estimating long-term mean recruitment levels (Walters and Martell 2004). One possible result of the mismatch in the scale of management to the scale of population processes is overexploitation in some local populations and under-exploitation in others, a phenomenon Prince et al. (1998) referred to as the “tyranny of scale.” A manager who has control over only a single local population will generally overexploit that local population in the context of sustaining the highest harvest across the entire metapopulation even if the metapopulation dynamics are known, because the local manager will not take into account the impacts of local harvest on larval export (Costello and Polasky 2008, Costello and Kaffine 2010, White and Costello 2010). Fishery management priorities can differ depending on whether a local population is considered to be open vs. closed (White et al. 2013), so it is imperative that recruitment dynamics are considered to achieve effective management of marine resources.

Small-scale coral reef fisheries are exemplary of fisheries that harvest at the local population scale. Most coral reef fishers target local populations of reef fishes or invertebrates (including gastropods, molluscs, echinoderms, and crustaceans). They provide income and food security to communities throughout the tropics and subtropics, and many countries are dependent on these fisheries and vulnerable to their declines from a food security perspective (Hughes et al. 2012), yet over half of the small-scale coral reef fisheries in island nations are being harvested unsustainably (Newton et al. 2007). These fisheries are notoriously difficult to manage due to a lack of institutional support, centralized landing

locations, biological data, and data on harvest rates and fishing mortality (Mahon 1997, Parma et al. 2003). Adding to these management challenges are the fact that most coral reef fisheries occur and are managed on spatial scales that likely exhibit mixed recruitment: Coral reef organisms frequently have complex life histories with pelagic larvae that settle locally or disperse to other reefs depending on larval behavior, the availability of settlement substrate, and myriad biological factors (Cowen et al. 2006). Thus, managing multiple local populations as distinct management units is logistically, institutionally, and financially difficult, especially if there is little information about whether recruitment dynamics of a local stock are primarily open or closed.

Here we tested whether and how management priorities for a small-scale coral reef fishery change based on the local population structure determined by the level of self-recruitment, using high-quality empirical data and accompanying models. We examined a small-scale coral reef fishery targeting giant clams (*Tridacna maxima*) on the island of Moorea, French Polynesia, as a test case because of the biology of giant clams and the nature of their fisheries. Giant clams (family Tridacnidae), or “pahua” in Tahitian, are similar to many other coral reef-associated organisms in that they are broadcast spawners with a pelagic larval stage during which dispersal and transport occur. Their short pelagic larval duration of 7–11 days (Jameson 1976) makes it likely that local populations exhibit a mix of self-recruitment and external recruitment. They are protandrous hermaphrodites and easily tracked through time because they are sessile once settled onto substrate. Munro (1993) and Lucas (1994) provide reviews of giant clam life cycles and general biology and morphology. Giant clam fisheries operate on coral reefs throughout the Indo-Pacific region (Villanoy et al. 1988), usually as local subsistence or small-market fisheries. As human populations and markets have expanded in Oceania, giant clams have been extirpated on several islands due to overharvest (Lucas 1994). Clearly there is a need for further scientific research to aid the management of small-scale fisheries that target local marine populations and upon which many people and cultures depend.

METHODS

General approach

We combined empirical data and population modeling to evaluate whether management priorities can vary depending on recruitment assumptions of open vs. closed. We gathered empirical data on growth, fecundity, survival, and recruitment for giant clams in our model system to parameterize two population models, a closed (100% self-recruitment) model and an open (0% self-recruitment) model. We start by describing the range of local dynamics under recruitment uncertainty by modeling the extremes of self-recruitment (closed and open) and calculating the self-recruitment transition

FIG. 1. Map of Mo'orea and Tetiaroa within the Society Islands, French Polynesia. Study sites are indicated with black diamonds, and reef is white outlined in black.

point, defined as the level of self-recruitment (expressed as the number of self-recruits produced per unit of local gonad biomass) above which the population exhibits self-sustaining (corresponding to closed) dynamics, and below which the population exhibits non-self-sustaining (corresponding to open) dynamics. Calculating the self-recruitment transition point allowed us to describe the range of possible dynamics of a local population because it describes the recruitment conditions under which the local population exhibits self-sustaining vs. non-self-sustaining dynamics. Then we compared management priorities using future population abundance in 20 years as a management target by calculating the elasticities of demographic rates to future abundance from each of the two models. We also reconstructed unfished population dynamics under a range of hypothesized harvest rates because no estimates of fishing mortality rates exist for this fishery.

We used size-based integral projection models (IPMs) to simulate population dynamics of giant clams (Easterling et al. 2000, Ellner and Rees 2006). IPMs are similar to matrix population models that have been used extensively for conservation biology (Morris and Doak 2002), including for assessing fisheries and determining the effects of harvest on population sustainability (e.g., Crouse et al. 1987, Moloney et al. 1994, Freckleton et al. 2003). IPMs differ from matrix models because they characterize individuals by a continuous individual-level state variable such as size or age (Easterling et al. 2000, Ellner and Rees 2006), and consequently IPMs more accurately estimate population sensitivities (Easterling et al. 2000) on which management decisions are often based (e.g., Crowder et al. 1994). Additionally, IPMs are

suitable for fisheries that lack good time series of stock and harvest (as is the case for many small-scale fisheries), because they require only basic biological data on growth, survival, and reproduction. We illustrate the utility of IPMs in marine systems, at the local population scale under uncertainty in self-recruitment, and for a harvested population. Our study illustrates that, in order to describe the dynamics of a local marine population, there is no need to explicitly model a mix of self-recruitment and external recruitment, nor to empirically determine the ratio of self-recruitment to total recruitment. Our approach is novel in modeling the effects of an unknown fishing mortality rate on the abundance of a local population with an unknown amount of self-recruitment.

Study system

We studied a local population of giant clams (*Tridacna maxima*) on the island of Mo'orea, the Society Islands, French Polynesia (Fig. 1; see Plate 1). In the waters around Mo'orea, this clam is harvested and managed as a distinct fishery. Mo'orea is surrounded by barrier reefs that form large lagoons of 0.5–5 m water depth, in which giant clams attach to hard substrate composed either of live or dead hard corals or basalt seafloor. Giant clams are sessile as adults, and are protandrous hermaphrodites and broadcast spawners (Lucas 1994). We expect that recruitment for the local population on Mo'orea is a mix of self and external based on (1) the short 7–11 day pelagic larval duration of giant clams (Jameson 1976), (2) the diameter of Mo'orea compared to the possible larval dispersal distance (~17 km across compared to a 10–200 km

dispersal distance; see Shanks et al. 2003), and (3) the probable local retention of larvae on Mo'orea driven by local scale (1–10 km) circulation patterns, which consists of wave-driven onshore movement of water from open water over the reef crest into the lagoon, the flow of water through the lagoon and back into open water through multiple passages, and the recirculation of some water back into the lagoon through mixing and subsequent wave-driven re-entry into the lagoons (Hench et al. 2008).

Mo'orea has the second highest human population (~17 000) of the French Polynesian islands (ISPF 2007), and there is widespread small-scale harvest for giant clams that are generally consumed locally (A. Yau, *personal observation*). Fishers harvest giant clams while snorkeling, dislodging the clams from substrate by using a screwdriver or other long, sharp object to pierce the byssal organ through the incurrent siphon orifice. Harvest of giant clams on Mo'orea is regulated by no-take marine reserves established in 2002 and a minimum size limit of 120 mm (PGEM 2005) shell standard length (SL), which is the maximum anterior–posterior distance, excluding shell scutes. However, the size limit and reserves are virtually unenforced, and thus only marginally functional, although there is minimal self-regulation by fishers and tourism operators (A. Yau, *personal observation*).

We also surveyed clams on the nearby island of Tetiaroa to supplement our data set with relatively large clams >100 mm SL, which are rare on Mo'orea. Tetiaroa is a private island located 55 km to the northeast of Mo'orea (Fig. 1), which had only minimal giant clam harvesting before and during the study period. We included growth data from Tetiaroa for fitting growth functions in the models, but did not include Tetiaroa clams in our abundance measurements and modeled only the clams on Mo'orea as a distinct local population.

Sampling design

We monitored giant clams from 12 sites on Mo'orea and two sites on Tetiaroa (Fig. 1), and used the demographic data we collected on growth, survival, and recruitment as a microcosm of the population dynamics on Mo'orea. Sites were located throughout the lagoon on Mo'orea, specifically in the back reef (adjacent to the reef crest), patch reef (mid-lagoon), or fringing reef (adjacent to shore). We found no differences in demographic rates and patterns with site or habitat type, so all data were pooled for model fitting. At each site, we established 2–4 permanent transects (30 × 2 m) placed parallel to shore and tagged the substrate immediately adjacent to each clam on each transect with a unique three-letter tag made from alphabet beads embedded in Z-spar compound (Splash-zone A788; Kopcoat, Pittsburgh, Pennsylvania, USA) and a small nail to provide a three-dimensional marker. We also recorded the color and exact location of each clam on

each transect to facilitate repeated individual measurements.

We measured demographic rates of growth, survival, and recruitment by marking and repeatedly measuring 1949 individual clams annually during Austral winter (June–August) from 2006 to 2010. At Tetiaroa, clams were measured from 2008 to 2010. This difference in the sampling periods was of little consequence because we pooled data across years for IPM fitting (see next sections). Clams were characterized by their size, measured as shell SL, which is related to biomass in this species as a power function (Gilbert et al. 2006; A. Yau, *unpublished data*). We measured annual growth increments by recording the SL of each individual clam to the nearest 0.1 mm each year. Survival was measured as the presence (survival) or absence (death) of a clam at each substrate tag and nail. This survival measured total mortality, including both natural and fishing mortality in unknown proportions; the inclusion of these survival measurements in our population models thus included both natural and fishing mortality sources. Fewer than 10% of the clams surveyed on Mo'orea and Tetiaroa were >100 mm, so to further increase the accuracy of growth and survival estimates for large clams we individually tagged and measured additional clams >100 mm throughout the lagoon of Mo'orea. We chose these clams from inside the study area but outside established transects, and measured them from 2008 to 2010. The GPS location of each large clam was recorded and used to relocate individuals in subsequent years.

Recruitment was quantified annually as the total number and size of recruits found on each transect that were not present the previous year. We defined recruits as clams ≤50 mm that had settled out from the pelagic larval stage and metamorphosed, because clams >50 mm were considered ≥1 year old based on growth rates reported by Munro (1993) and Hart et al. (1998). We remeasured the SL and survival of recruits during subsequent years. In this way, we accounted for every clam on each transect during our study period. To quantify local fecundity (measured as gonad dry mass), we estimated the relationship between gonad biomass and size. In August of 2008 and 2010, we collected clams spanning the size range from outside the permanent transects on both islands, measured their SL, dissected them to separate gonads from somatic tissue, and dried the tissues in an oven at 80°C for 48–72 hours.

Integral projection model

We fit a size-based IPM (Easterling et al. 2000, Ellner and Rees 2006) for giant clams on Mo'orea, matching the scale of local population modeling with the island scale of management. First, we constructed a closed population model assuming recruits are offspring of local adults, which generally takes the form $N_{t+1} = \lambda N_t$, where N_t is the population abundance at time t , and λ is the intrinsic rate of population growth that includes individual growth, survival, and self-recruitment. IPMs

describe individuals as a continuous state variable x , in this case clam SL. IPMs describe a population N_t as a continuous distribution function $n(x, t)$ that represents the number of individuals in the range $[x, x + dx]$ at time t . Abundance at a given time step can be calculated by integrating $n(x, t)$. The general IPM equation is

$$\begin{aligned} n(y, t + 1) &= \int_L^U K(y, x) n(x, t) dx \\ &= \int_L^U (P(x, y) + F(x, y)) n(x, t) dx \quad (1) \end{aligned}$$

where $[L, U]$ is the range of possible sizes, $K(y, x) = P(x, y) + F(x, y)$ is the projection kernel, P is survival and growth from size x to size y , and F is self-recruitment or the production of size y self-recruits from size x parents. The kernel is analogous to a projection matrix in matrix population models, representing all possible size transitions including self-recruitment, and can be used to calculate the continuous size distribution of individuals in the next time step given the size distribution in the current time step. We assumed a maximum size of 200 mm for *T. maxima* in our system because only 7 of the 1949 clams that we sampled were >150 mm, with a maximum observed size of 184 cm. The range of possible sizes is 1 to 200 mm.

Second, we modified the closed IPM in Eq. 1 to create an open IPM. In an open population, observed recruits are offspring of external adults, so recruitment levels are modeled as independent of the local adult population: $N_{t+1} = \lambda N_t + R_{t+1}$, where λ only includes survival and growth, and R_{t+1} is the pulse of external recruits. The analogous IPM equation is

$$\begin{aligned} n(y, t + 1) &= \int_L^U K(y, x) n(x, t) dx + R(y, t + 1) \\ &= \int_L^U P(x, y) n(x, t) dx + R(y, t + 1) \quad (2) \end{aligned}$$

where $K(y, x)$ no longer includes the self-recruitment function F , and $R(y, t + 1)$ is a continuous distribution function representing the external pulse of recruits of size y entering the population at time $t + 1$.

Growth and survival are modeled the same way in the closed and open models. The growth-survival function $P(x, y)$ consists of two separate components (growth and survival) multiplied together. We used measurements of growth from both Mo'orea and Tetiaroa to model growth from size x to size y as the growth increment form of the von Bertalanffy equation (Fabens 1965), $g(x, y) = a_g + b_g x$, by estimating both the expected growth and variance in growth of a size x individual. We estimated the expected growth parameters using an ordinary least squares regression of size at time $t + 1$ on size at time t . We estimated the conditional variance, $\text{var}(y) = a_v + b_v x$, using least squares regression of the squared residuals from the first regression on size at time t . In both cases, we selected a linear form for the

relationship after testing the significance of a nonlinear term using a type III sum-of-squares test.

Using survival data from Mo'orea that measured total mortality including both natural and fishing sources, we used nonlinear logistic regression to model survival, $s(x)$, to the next time step as a function of size: $\log(s(x)/(1 - s(x))) = a_s + b_s/(x + c_s)$, using nonlinear minimization to minimize the AIC_c of the model (see Appendix A for survival fitting methods). We chose this functional form based on our data, to allow survival to increase as recruits grew into juveniles, then asymptote to a value less than one as clams reached the largest sizes. Because our estimates of survival rates include total mortality from both natural and fishing sources, projections from the IPMs predict abundance under the present unknown fishing mortality rate. The fitting of growth and survival functions to observed data was completed in R version 2.10.1 or higher (R Development Core Team 2009).

Closed population model

Under the assumption that all recruitment in the local population is derived from local adults, we estimated $F(x, y)$ by partitioning the number of observed recruits in a given year among reproductive clams in the previous year, in proportion to their relative fecundity (Brazero and Defeo 1999). Using ordinary least squares regression, we regressed the log of gonad dry mass on the log of clam size to estimate a power relationship for size-dependent relative fecundity, and used this to estimate the total gonad dry mass of reproductive individuals within our transects each year. For each year that we measured recruitment on Mo'orea (2007–2010), we calculated the ratio of recruits in our transects (assuming all were self-recruits) to the total gonad dry mass of reproductive individuals (calculated as >66.1 mm SL) in transects the previous year, then averaged this ratio across years to obtain a conversion factor c_f . The result is a power function expressing the total number of self-recruits (across all recruit sizes) produced by an adult clam of size x : $f(x) = a_f c_f x^{b_f}$. We modeled the size of recruits y independent of adult size x , as a normal distribution with mean and standard deviation calculated from observed data on all recruits.

When the closed IPM model is projected through time, the population converges to a stable size distribution, at which point abundance grows ($\lambda > 1$, “self-sustaining”) or declines ($\lambda < 1$) geometrically. We report λ and the stable size distribution following methods by Ellner and Rees (2006), and also calculated the time required to come within 0.01% of the stable size distribution. To construct confidence intervals for λ , we bootstrapped the original population by sampling with replacement and re-calculated λ over 1000 bootstrap replicates.

To evaluate management priorities, we projected future population abundance for 20 years starting from the size distribution of clams in transects on Mo'orea averaged over the study period (2006–2010) and

calculated the elasticities to future abundance for each demographic rate of growth, survival, and self-recruitment in $K(y, x)$ in Eq. 1. An elasticity value is a proportional change in a model output (in this case, future population abundance at year 20) for a given change in a model parameter value, and is calculated by changing a given demographic rate by a given proportion (1% increase in this case) and measuring the resulting proportional change in future abundance. Higher elasticities are indicative of demographic rates that more strongly influence future abundance. Using these elasticity values, we then calculated (1) total survival elasticity for a clam of a given size at time t by integrating elasticities for all possible transitions for that clam (functionally, by integrating all “columns” of $K(y, x)$ for each size x), and (2) total recruitment elasticity for a recruit <50 mm of a given size at time $t + 1$ by integrating elasticities for all possible transitions resulting in that clam (functionally, by integrating all “rows” of $K(y, x)$ for each recruit size y). We chose a 20-year time horizon to allow both the closed model to reach the stable size distribution, and the open model to reach equilibrium abundance. Note that total elasticities of demographic rates to future abundance integrate to the time horizon ($t = 20$ years) (Fox and Gurevitch 2000), and not to 1 as is the case for the more commonly presented elasticities of λ (de Kroon et al. 2000). Statistical modeling, IPM simulation, and subsequent analyses were performed in MATLAB 7.6.0.324 with Statistics Toolbox 6.2 (MathWorks 2008).

Open population model

Under the assumption that none of the recruitment in the local population is derived from local adults, we modeled external recruitment $R(y, t + 1)$ from Eq. 2 as an annual pulse of recruits equal to the average number of recruits observed across years (2007–2010), and the size of recruits y as a normal distribution with mean and standard deviation calculated from observed data on all recruits. Open populations eventually reach an equilibrium abundance (see Hughes 1990), which we define for calculation purposes as annual change in abundance $<0.01\%$, and which we refer to as “non-self-sustaining.” Starting with the average size distribution and abundance of clams in transects on Moorea over the duration of the study period (2006–2010), we iterated the model until equilibrium abundance N_{eq} was reached. We also constructed confidence intervals for N_{eq} by bootstrapping the original population, sampling with replacement and re-calculating N_{eq} over 1000 bootstrap replicates.

Similar to methods for evaluating management priorities in the closed model, we projected future population abundance for 20 years starting from the average annual size distribution of clams in transects on Moorea and calculated the elasticities for future abundance for each demographic rate of growth and survival in $K(y, x)$ from Eq. 2. Additionally, we calculated elasticities to abundance in 20 years for each

external recruitment value in $R(y, t + 1)$ from Eq. 2. Using these elasticity values, we then calculated (1) total survival elasticity for a clam of a given size at time t by integrating elasticities for all possible transitions for that clam (functionally, by integrating all “columns” of $K(y, x)$ for each size x), and (2) total recruitment elasticity for a recruit <50 mm of a given size at time $t + 1$ by integrating elasticities for all possible transitions resulting in that clam (functionally, by integrating all “rows” of $K(y, x)$ and $R(y, t + 1)$ for each recruit size y). Again, total elasticities of demographic rates to future abundance do not integrate to 1 as is the case for the more commonly presented elasticities of λ (de Kroon et al. 2000). However, total elasticities of recruitment to equilibrium abundance in an open model should integrate to 1 (Appendix B).

Transition from self-sustaining to non-self-sustaining dynamics

We calculated the transition between self-sustaining and non-self-sustaining dynamics by reducing parameter c_f (the ratio of self-recruits:dry gonad) in the self-recruitment term of the closed model until self-recruitment balanced deaths ($\lambda = 1$). We denote this critical value as c_f^* , to represent the number of self-recruits produced per unit of local gonad biomass required to maintain local abundance.

If $c_f > c_f^*$ for a local population, the population growth factor increases with increasing levels of self-recruitment, controlled by c_f . Population abundance will exhibit self-sustaining dynamics and increase geometrically. However, if $c_f < c_f^*$ for a local population, the population will exhibit non-self-sustaining dynamics by reaching an equilibrium abundance where total annual recruitment (self-recruitment + external recruitment) balances annual deaths. Changing the value of c_f does not reflect an actual decrease in reproductive output per unit of gonad biomass, which is likely to remain constant, but instead reflects a change in the number of recruits produced that become self-recruits. The value of the self-recruitment transition point can determine the likelihood of a local population exhibiting self-sustaining vs. non-self-sustaining dynamics (see *Discussion*).

Reconstruction of unfished populations

The observed survival of giant clams on transects in the Moorea population is a measure of total mortality from both natural and fishing sources in unknown proportions. We could not determine actual fishing mortality rates due to the lack of a fishery monitoring program and centralized landing ports. However, we characterized the size distribution of fishing mortality on Moorea in two ways: (1) measurement of recently discarded shell piles and (2) direct measurement of catch. Fishers harvest giant clams in their shell before shucking a day’s harvest in one spot, leaving piles of shells in the lagoon. These shell piles are highly visible from the surface due to the contrast of bright white shell

FIG. 2. Size distributions of individual giant clams (*Tridacna maxima*) sampled from sites on (A) Mo'orea and (B) Tetiaroa, showing truncation on Mo'orea at larger sizes. The legal minimum size limit is indicated by a black line at 120 mm. (C) Size distributions of harvest on Mo'orea, obtained through measurements of discarded shell piles and shells measured directly during fishing events.

interior against the darker colors of sand, rubble and coral (A. Yau, *personal observation*). From June to August 2008–2010, weekly surveys of the entire study area were conducted by boat. During these surveys, we collected and measured shell piles less than one year old (determined based on the degree of algal growth and other encrusting organisms inside the shell) to construct a size distribution of harvest. We also surveyed fishers in the lagoon waters of the study area and measured the size distribution of their catch in situ.

We estimated unfished population dynamics under three plausible scenarios of fishing mortality, assuming that such mortality constitutes 10%, 25%, or 50% of the total annual observed mortality across the size range of harvested clams (>50 mm). For each year of the study under each of the three scenarios, we calculated the expected number of clams harvested from the transects, randomly selected that many clams from the harvest size distribution, re-inserted them into the population data set, and recalculated the size-dependent survival function. The actual fishing mortality rate probably lies somewhere in this range (i.e., 0–50%) of hypothetical fishing mortality rates, and is definitely >0%. We repeated the process of selecting and re-inserting harvested individuals back into the population 1000 times for each scenario, and calculated mean survival

function parameters from these replicates. All other functions and fittings for growth, self-recruitment, and external recruitment remained the same as in the original models.

For each fishing mortality scenario, we used the mean survival parameters to predict the population growth factor (λ), stable size distribution, and time to reach the stable size distribution in a self-sustaining population, and to predict the equilibrium abundance, equilibrium size distribution, and time to equilibrium in a non-self-sustaining population.

RESULTS

Surveys

We marked and tracked 1949 individual giant clams (*Tridacna maxima*) in 44 transects on Mo'orea and Tetiaroa that covered 2430 m² over the five-year period. This resulted in a total of 1779 measurements of survival on Mo'orea, 1330 measurements of growth on Mo'orea and Tetiaroa, and 658 recruits recorded on Mo'orea (included in the total number of tracked individuals). Our resighting rate was ~99% (21 clams subsequently known to be alive were missed in a previous year). We tagged and remeasured 57 large clams >100 mm on Mo'orea outside of transects to obtain an additional 91 measurements of survival and 70 measurements of growth in this size range over a three-year period. A total of 159 clams were collected and dissected to determine the gonad biomass–size relationship. The average annual abundance from the transect area of 2160 m² on Mo'orea was 729 ± 53 clams (shown are all mean $\pm$ SE), with an average density of 0.57 ± 0.03 clams/m² suitable substrate, defined as hard substrate excluding sand and coral rubble.

Less than 3% of the clams we observed on Mo'orea were larger than 120 mm, the legal minimum size limit (Fig. 2A). The size distribution of clams on Mo'orea is significantly different from the size distribution on the relatively unfished island of Tetiaroa (Fig. 2B), where 15% of the observed clams are larger than the size limit (Kolmogorov-Smirnov two-sample test, $P < 0.0001$). The size distribution of harvest on Mo'orea indicates that fishers target and remove clams as small as 50 mm (clams <66 mm are pre-reproductive), and almost 80% of harvested clams are smaller than the minimum size limit of 120 mm (Fig. 2C). The average clam size at harvest is 104.7 ± 0.7 mm ($n = 782$). Each discarded shell pile or fishing event consisted of 77.4 ± 12.5 clams ($n = 14$).

Estimated IPM function and parameters

All demographic rates were strongly size dependent. Survival increased as clams grew from recruits (15–50 mm) into juveniles (~50–80 mm), then leveled off as clams grew from ~80 mm to 200 mm (Table 1, Fig. 3A). Mean size at time $t + 1$ increased linearly with size at time t (Table 1, Fig. 3B). Based on this growth function, a clam requires 10 years to reach the minimum legal size

TABLE 1. Statistical results of fitting functions and parameters used for survival ($s(x)$), growth ($g(x, y)$), variance in growth ($\text{var}(y)$), recruit size, fecundity in the closed model ($f(x)$), and external recruitment in the open model for giant clam integral projection models.

Functions	Equation	a_i ($\pm$ SE)	b_i ($\pm$ SE)	df	r^2	F	P
Survival	$\log\left(\frac{s(x)}{1-s(x)}\right) = a_s + \frac{b_s}{(x+3.86)}$	1.29 (± 0.11)	-19.14 (± 4.38)	1777		-4.365†	<0.0001
Growth	$g(x, y) = a_g + b_g x$	21.15 (± 0.44)	0.869 (± 0.0064)	1328	0.93	18282.86	<0.0001
Variance in growth	$\text{var}(y) = a_v + b_v x$	68.45 (± 6.06)	-0.275 (± 0.088)	1328	0.0073	9.81	0.0018
Recruit size	$N(\mu, \sigma^2)$	28.3 (± 10.6 mm)‡					
Closed model							
Fecundity	$f(x) = a_f c_f x^{b_f}$	5.64×10^{-8} ($\pm 1.30 \times 10^{-8}$)§	3.63 (± 0.09)	148	0.91	1571.06	<0.0001
Open model							
External recruitment		198 (± 59 recruits)					

Notes: The variable x represents a clam of size x in any given year. Parameters a , b , and c were calculated for each function (survival, growth, variance, fecundity), specified by subscripts.

† Represents the t statistic of b_s rather than the F statistic.

‡ Represents the mean (μ) and standard deviation (σ^2) for the normal distribution (N).

§ Represents $a_f c_f$.

of 120 mm. Von Bertalanffy growth parameters calculated from this function ($K = 0.14$, $L_{\text{inf}} = 161.9$ mm) lie within the range of parameter values for *T. maxima* summarized by Smith (2011) ($K = [0.074, 0.28]$, $L_{\text{inf}} = [124 \text{ mm}, 305 \text{ mm}]$). The residuals for the growth regression are approximately normal, but the variance declines linearly with clam size (Table 1, Fig. 3C).

The total number of recruits on Mo'orea pooled across all 12 sites over 2160 m² in each year from 2007 to 2010 was 178, 362, 167, and 84 recruits, respectively. Dry gonad biomass increased exponentially as a function of size: $y = (3.84 \times 10^{-8})x^{3.63}$ (Fig. 3D). This function was converted into the fecundity component $f(x)$ of self-recruitment in the closed model using the conversion factor, $c_f = 1.467$ self-recruits per gram of dry gonad. The fecundity component of the closed model describes the number of self-recruits produced per adult, with a minimum reproductive size of 66.1 mm based on our observations (Table 1). Annual external recruitment was set to the mean level of 198 ± 59 recruits in the open model, and recruit size in both the closed and open IPMs was modeled as a normal distribution with mean 28.3 and standard deviation 10.6 mm, independent of adult size (Table 1).

Closed IPM

The projection kernel $K(y, x)$ describing all possible size transitions has a narrow ridge just above the one-to-one line representing survival and growth, and a broad ridge in the lower right representing self-recruitment (Fig. 4A). Just as in most matrix models, the values associated with self-recruitment are larger than those for growth-survival; production of self-recruits by the

largest individuals is an order of magnitude higher than values for the growth-survival component reflecting the high fecundity of giant clams. With the estimated demographic functions, the asymptotic population growth factor is $\lambda = 1.07$; bootstrap 95% confidence intervals for λ are [1.04, 1.10], and indicating that, if it is closed, the population is projected to increase under present conditions (with fishing mortality included in the model's total mortality estimates). The stable size distribution for the closed population (Fig. 4B) was reached after 10 years, and is dominated by recruit-sized individuals, with 5.1% of the population larger than the minimum legal harvest limit of 120 mm. The shape of the reproductive value distribution reflects the increase in fecundity as a power function of size (Fig. 4B).

Of all demographic rates, total elasticities to future abundance were highest for survival of mid-sized clams ranging from ~80–120 mm SL (Fig. 5), with a maximum elasticity value of 0.123 for 95.5-mm SL clams. Thus, a 1% increase in the survival of these clams will yield a 0.123% increase in future population abundance in 20 years. Overall recruitment elasticities were slightly less than survival elasticities (Fig. 5B), with a maximum elasticity value of 0.0924 at 49.8 mm SL (essentially 50 mm, the cutoff for maximum recruit size).

Open IPM

For the open IPM, the equilibrium abundance for the Mo'orea population is projected to be 680 individuals, equivalent to 93.4% (bootstrap 95% confidence intervals [86.5%, 101.8%]) of the observed mean of 729 ± 53 clams from 2160 m² sampled. Starting from the observed mean abundance and size distribution, the model reaches

TABLE 2. Statistical results of fitting survival functions ($s(x)$) upon removal of fishing mortality rates that are an assumed percentage of total mortality.

Fishing mortality (% of total mortality)	Equation	a_s ($\pm$ SE)	b_s ($\pm$ SE)
10	$\log\left(\frac{s(x)}{1-s(x)}\right) = a_s + \frac{b_s}{(x+3.86)}$	1.47 ($\pm 3.18 \times 10^{-5}$)	-24.28 (± 0.0018)
25	$\log\left(\frac{s(x)}{1-s(x)}\right) = a_s + \frac{b_s}{(x+3.86)}$	1.75 ($\pm 3.58 \times 10^{-5}$)	-32.71 (± 0.0024)
50	$\log\left(\frac{s(x)}{1-s(x)}\right) = a_s + \frac{b_s}{(x+3.86)}$	2.35 ($\pm 1.63 \times 10^{-5}$)	-50.34 (± 0.0017)

Notes: The variable x represents a clam of size x in any given year. Parameters a_s and b_s were calculated for each survival function.

equilibrium after $t_{eq} = 19$ years. The size distribution at equilibrium is more skewed towards larger individuals than either the observed distribution or the closed IPM, with 9.0% of the population larger than the minimum size limit of 120 mm (Fig. 4B). The differences in asymptotic size distribution between the closed and open models can be explained by the difference in growth factor: The growing closed population has a higher proportion of younger, and hence smaller, individuals than the open population (Fig. 4B).

In contrast to the closed model, where total elasticities were highest for survival, total elasticities to future abundance for the open model were highest for recruitment of average-sized recruits, with a maximum elasticity of 0.0498 at size 30.5 mm (Fig. 5). A 1% increase in recruits of this size will result in a 0.0498% increase in future population abundance in 20 years. Survival elasticities were an order of magnitude smaller than those for recruitment, with a maximum survival elasticity of 0.0253 for juvenile clams at 55.1 mm (Fig. 5A).

Transitioning from self-sustaining to non-self-sustaining dynamics

The transition from self-sustaining (closed) to non-self-sustaining (open) dynamics occurs at $c_f^* = 0.775$ self-recruits per gram of dry gonad, which is 52.85% of the c_f value of 1.467 estimated under the assumptions of the closed model. Therefore, the transition point for giant clams on Mo'orea over the study period is equivalent to 52.85% self-recruitment out of the present total observed recruitment; this exact proportion will vary based on the abundance and recruitment level. The lowest abundance predicted for this local population from both models is an equilibrium abundance that is 93.4% of initial abundance at 0% self-recruitment, assuming that observed fishing mortality and recruitment levels persist over time.

Reconstruction of unfished populations

Removing fishing mortalities of 10%, 25%, and 50% of the total mortality of harvest-sized individuals increased the survival of clams >30 mm (Table 2, Fig. 6A). In the closed model, removing fishing mortality

increased the population growth factor λ from its baseline level, reaching 1.19 at 50% fishing mortality (Fig. 6B). Removing fishing mortality increased the time to reach the stable size distribution by up to one year, and had very little effect on the shape of the distribution.

For the open model, removing fishing mortality did not change the time to equilibrium ($t_{eq} = 19$ years), but increased the equilibrium population abundance, reaching 139.8% of average observed abundance at a 50% fishing mortality rate (Fig. 6B). In contrast to the closed model, removing fishing mortality in the open model shifted the asymptotic size distribution towards larger sizes (Fig. 6C).

DISCUSSION

Our elasticity analysis shows that management priorities vary depending on whether the population is expected to exhibit self-sustaining (closed) vs. non-self-sustaining (open) dynamics, under a management goal of increasing future population abundance in 20 years. Under self-sustaining dynamics, a manager should encourage survival of mid-sized clams ranging from ~ 80 –120 mm for the greatest positive impact on future population abundance. Ensuring higher survival of these clams could be achieved by enforcing the legal minimum size limit of 120 mm and/or the no-take marine reserves. This result was confirmed by our simulations removing fishing mortality: The highest elasticity values for growth and survival of clams 80–120 mm coincide with the size distribution of harvested clams, and any reduction in fishing mortality and/or enforcement of regulations would result in increased survival and thus increased abundance. In contrast, under non-self-sustaining dynamics, managers should encourage survival of juvenile clams ranging from ~ 50 –60 mm for the greatest positive impact on future abundance. Future population abundance is actually most sensitive to increased external recruitment under non-self-sustaining dynamics, but external recruitment is likely out of the realm of managers' influence, while juvenile survival is not.

Our study emphasizes the need to consider and understand local recruitment dynamics in order to effectively manage a local marine population. It should

FIG. 3. Growth, survival, and self-recruitment components of both the closed and open integral projection model for giant clams, *Tridacna maxima*. (A) Survival modeled as a logistic regression (1 = survival, 0 = death), with data points plotted as crosses for visual clarity. (B) Growth modeled as a linear regression, with data points plotted as dots. (C) Variance of growth modeled as a linear regression of squared residuals against size, with data points plotted as dots. (D) Fecundity as dry gonad biomass, a component of self-recruitment in the closed model, as a power function of adult size, with data points plotted as dots. Dry gonad biomass was converted to an expected number of self-recruits based on a calculated conversion factor, c_F , the ratio of recruits in transects to the total gonad dry mass of reproductive individuals.

be noted that sustained harvest at the local population level is not likely to result in maximum sustained harvest at the metapopulation level because the local manager will not take into account the impacts of local harvest on larval export (Costello and Polasky 2008, Costello and Kaffine 2010, White and Costello 2010). However, given the challenges of empirically determining recruitment patterns, managers may never know the dynamics of the entire metapopulation and more than likely may be required to manage at the local population level because of institutional and logistical structures. Managers may also choose to manage at the local population level to match spatial heterogeneity in demographic processes such as growth and size at maturity, as in the case of Australian abalone (Prince et al. 1998). Our study provides a new scientific method for modeling and managing a local population without information about the larger metapopulation, and is broadly applicable to local populations of sedentary marine organisms that are managed on spatial scales that are smaller than recruitment scales.

Our findings suggest that small-scale harvest of giant clams on Mo'orea can continue at its present level without resulting in extirpation or drastic population decline. The lowest projected abundance of giant clams on Mo'orea is 93% of present abundance, if the local population is entirely open. This projection holds if the present level of fishing mortality and the average recruitment rate persist. This equilibrium abundance is not significantly different from the present abundance (95% CI [86.5%, 101.8%]).

Our reconstruction of unfished populations found that fishing mortality reduced the frequency of harvest-sized individuals >50 mm in the population and decreased abundance overall. Fishing mortality on Mo'orea is likely relatively high based on the significantly lower density of clams on Mo'orea compared to Tetiaroa (0.57 ± 0.03 clams/m² compared with 1.80 ± 0.24 clams/m², respectively). Further evidence of high fishing mortality includes the low proportions of legal-sized clams (3–9% of the population) presently on Mo'orea and predicted by both the closed and open

FIG. 4. (A) The estimated projection kernel $K(y, x)$ for the *Tridacna maxima* closed integral projection population model, showing all possible size transitions as the self-recruitment component (lower right corner) and growth-survival component (diagonal). (B) The stable size (solid line) and reproductive value (dotted line) distributions of the closed population model. Equilibrium size distribution for the open model (dashed line) is similar to the stable size distribution of the closed model, with slightly higher abundance of larger individuals.

models under observed fishing mortality, compared to the higher proportion of legal-sized clams (15% of the population) on the relatively unfished island of Tetiaroa. Thus, our simulations suggest that small-scale harvest is likely responsible for the reduced densities and reduced proportion of legal-sized clams on Mo'orea where giant clams are no longer giants.

We assumed no other sources of density dependence in our IPMs because we projected from an initial low abundance over short time scales (<20 years). The strength of any density-dependent mechanism is likely to be low in this system because the present abundance on Mo'orea is likely below "virgin" pre-fishery abundance: Densities on Mo'orea are low compared to Tetiaroa and compared to the high densities of up to 224 giant clams/ m^2 documented elsewhere in the Pacific (Salvat 1971, as cited in Andrefouet et al. 2005). Giant clams also have the ability to grow on top of one another (Andrefouet et

al. 2005), furthering the potential for increases in giant clam abundance. Density-dependent survival has been described for juvenile giant clams aggregated in high densities (Hamner 1978), but was not found under low densities (Apte and Dutta 2010). Growth of Mo'orea's giant clam population from a relatively low abundance is likely to be geometric as we have modeled here, at least in the short term. Expanding to longer time horizons and higher abundances may require the incorporation of a mechanism for density dependence.

We could not determine definitively whether the local population of giant clams on Mo'orea is more likely to exhibit self-sustaining vs. non-self-sustaining dynamics. The similarities between the size distribution of Tetiaroa and the size distribution of the open model on Mo'orea with 50% fishing mortality removed (Figs. 2B and 6C) suggest that the population exhibits non-self-sustaining dynamics as in an open population. However, the size

FIG. 5. Elasticities of future population abundance in 20 years to (A) survival and (B) recruitment, for the closed (solid line) and open (dashed line) integral projection models for giant clams, *Tridacna maxima*.

distribution of the closed model with 50% fishing mortality would probably also become similar to the size distribution of Tetiaroa if a form of density dependence was included, allowing a closed population to reach an equilibrium abundance. The size distribution of the closed model is consistently dominated by younger individuals because the population is growing, but at equilibrium, the frequency of larger individuals in the population would increase.

The transition point between self-sustaining and non-self-sustaining dynamics indicates the relative importance of self-recruitment in a local population at a given recruitment level. We found the transition point at 0.775 self-recruits per gram of dry gonad, which is equivalent to 52.85% self-recruitment at the present population abundance and recruitment level. We cannot directly use the transition point to determine whether the local population exhibits one dynamic vs. the other because the transition point exists almost directly in the center of the range of self-recruitment at 52.85%. However, the proximity of the transition point to the extremes of the self-recruitment range (0% vs. 100%) is informative for scientists and managers in deciding whether the dynam-

ics of their local population of interest are self-sustaining or non-self-sustaining. For example, if a population with a relatively short pelagic larval duration and/or short dispersal distances has a transition point of 15% self-recruitment, then it is highly likely that >15% of recruits are self-recruits and the population will exhibit self-

FIG. 6. (A) Reconstructed survival functions from simulated removal of fishing mortalities expressed as a percentage of total mortality, obtained by replacing fished individuals back into the population. Survival was modeled as a logistic regression (1 = survival, 0 = death). (B) Population growth factors (λ , triangles) for the closed IPM increased as simulations removed 10%, 25%, and 50% of total mortality of harvest-sized individuals. Equilibrium abundance for the open IPM, expressed as a percentage of initial abundance (circles), increased as simulations removed increasing fishing mortalities. (C) Equilibrium size distributions for an open population, simulating the removal of 0%, 10%, 25%, and 50% of total mortality of harvest-sized individuals; see Fig. 6A for key.

PLATE 1. The giant clam *Tridacna maxima* attaches to hard substrate in the coral reef waters around Mo'orea, French Polynesia. Photo credit: A. J. Yau.

sustaining dynamics. Calculating this transition point is a good alternative to empirically estimating the amount of self-recruitment, given that population models only require basic data on growth, survival, fecundity, and recruitment for construction of a closed model, and part or all this data may already be available for a given system.

The approach we used to determine management priorities and describe the dynamics of a local population under uncertainty in the amount of self-recruitment can be applied to any species with sessile or sedentary adults and a pelagic larval stage, harvested or not. Our approach is also applicable to many small-scale fisheries worldwide that are managed at the local scale but have no information on fishing mortality rates or the amount of self-recruitment. Studies such as this can be used to inform the management of small-scale fisheries that are globally important due to their prevalence and the high dependence of fishery participants for food and income. The continued ability of small-scale fisheries to provide resources to humans are dependent on management decisions informed by quantitative studies assessing management priorities, population dynamics, and effect of fishing on local populations.

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SUPPLEMENTAL MATERIAL

Appendix A

Fitting survival models in an integral projection model for giant clams, *Tridacna maxima* ([Ecological Archives A024-087-A1](#)).

Appendix B

Elasticity of equilibrium abundance to recruitment in an open model sums to one ([Ecological Archives A024-087-A2](#)).