



Cost-Effectiveness of Alternative Conservation Strategies with Application to the Pacific Leatherback Turtle

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Abstract: *Although holistic conservation addressing all sources of mortality for endangered species or stocks is the preferred conservation strategy, limited budgets require a criterion to prioritize conservation investments. We compared the cost-effectiveness of nesting site and at-sea conservation strategies for Pacific leatherback turtles (*Dermochelys coriacea*). We sought to determine which conservation strategy or mix of strategies would produce the largest increase in population growth rate per dollar. Alternative strategies included protection of nesters and their eggs at nesting beaches in Indonesia, gear changes, effort restrictions, and caps on turtle takes in the Hawaiian (U.S.A.) longline swordfish fishery, and temporal and area closures in the California (U.S.A.) drift gill net fishery. We used a population model with a biological metric to measure the effects of conservation alternatives. We normalized all effects by cost to prioritize those strategies with the greatest biological effect relative to its economic cost. We used Monte Carlo simulation to address uncertainty in the main variables and to calculate probability distributions for cost-effectiveness measures. Nesting beach protection was the most cost-effective means of achieving increases in leatherback populations. This result creates the possibility of noncompensatory bycatch mitigation, where high-bycatch fisheries invest in protecting nesting beaches. An example of this practice is U.S. processors of longline tuna and California drift gill net fishers that tax themselves to finance low-cost nesting site protection. Under certain conditions, fisheries interventions, such as technologies that reduce leatherback bycatch without substantially decreasing target species catch, can be cost-effective. Reducing bycatch in coastal areas where bycatch is high, particularly adjacent to nesting beaches, may be cost-effective, particularly, if fisheries in the area are small and of little commercial value.*

Keywords: bycatch, economics, fisheries, nesting, noncompensatory mitigation, sea turtle

Rentabilidad de Estrategias de Conservación Alternativas Aplicadas a Tortugas Laúd del Pacífico

Resumen: *Aunque la conservación holística que aborda todas las causas de mortalidad de especies en peligro es la estrategia de conservación preferida, los presupuestos limitados requieren un criterio para priorizar las inversiones de conservación. Comparamos la rentabilidad de estrategias de conservación del sitio de anidación y de conservación en el mar aplicadas en tortugas laúd del Pacífico (*Dermochelys coriacea*). Tratamos de determinar cual estrategia o combinación de estrategias produciría el mayor incremento de la tasa de crecimiento poblacional por dólar. Las estrategias alternativas incluyeron la protección de anidantes y sus huevos en playas de anidación y criaderos, cambio de equipo en la pesquería de pez espada en Hawái (E.U. A.) y el cierre temporal y de áreas en la pesquería con redes agalleras en California (E. U. A.). Utilizamos un modelo poblacional con una métrica biológica para medir los efectos de las alternativas de conservación. Normalizamos todos los efectos para priorizar aquellas estrategias con el mayor efecto biológico en relación con su costo económico. Utilizamos simulación Monte Carlo para abordar la incertidumbre en las variables principales y para calcular la distribución de probabilidades para mediciones*

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de rentabilidad. La protección de la playa de anidación fue la forma más rentable para lograr incrementos en las poblaciones de tortugas laúd. Este resultado crea la posibilidad de la mitigación no compensatoria de la captura incidental, en la que las pesquerías con altos niveles de captura incidental invierten en la protección de playas de anidación. Un ejemplo de esta práctica son los procesadores de atún en E.U. A. y de los pescadores de California que utilizan redes agalleras que financian la protección de sitios de anidación. Bajo ciertas condiciones, las intervenciones de pesquerías, con tecnologías que reducen la captura incidental de tortugas laúd sin una disminución sustancial de la captura de la especie de interés, pueden ser rentables. La reducción de la captura incidental en áreas costeras donde es elevada, particularmente cerca de playas de anidación, puede ser particularmente rentable si las pesquerías en el área son pequeñas y con escaso valor comercial.

Palabras Clave: Anidación, captura incidental, economía, mitigación no compensatoria, pesquerías, tortuga marina

Introduction

Although holistic conservation addressing all sources of mortality for endangered species or stocks is the preferred conservation strategy (Dutton & Squires 2011), limited budgets require a criterion to prioritize conservation investments. Cost-effectiveness analysis (CEA) helps in the prioritization of conservation strategies by identifying the strategy that will have the greatest effect for a given cost. This is measured by the biological impact (benefit) divided by the action's economic cost. A CEA-derived conservation strategy or mix of strategies provides the largest increase in population growth rate per dollar of conservation investment. Strategies yielding the greatest effect, such as those with elasticities that indicate the largest increase in population growth rate per unit increase in survival, may be relatively costly, whereas other activities with a lower absolute effect may have a greater effect per dollar and thus provide better results for the same amount of money.

The collapse of Pacific leatherback (*Dermochelys coriacea*) populations is a result of at-sea mortality from fisheries bycatch and direct harvest and of egg and hatchling mortality due to loss of nesting habitat, nest predation, egg harvest, and other beach-related sources of mortality (Spotila et al. 2000; Tapilatu et al. 2013). Holistic conservation of this species includes conservation of nesting beaches to protect nesting females, their eggs, and critical breeding habitat and to maximize hatchling production; enhancement of at-sea survival of juveniles and adults by reducing turtle bycatch from industrial and artisanal fishing; and reducing subsistence take.

We compared cost-effectiveness of 3 strategies to protect the western Pacific leatherback turtle population: nesting beach protection in Papua, Indonesia; gear, effort, and turtle take regulations in the Hawaiian (U.S.A.) longline (HLL) swordfish fishery; and temporal and area closures in the California (U.S.A.) drift gill net fishery (CDGN). Part of the western Pacific leatherback population migrates from breeding areas in Indonesia to foraging areas across the North Pacific from Hawaii to California.

At the time of our study, there were no conservation projects focused on reducing bycatch of this population of leatherbacks from artisanal fisheries, so we could not estimate these costs. Thus, we focused on the other 2 strategies.

Methods

CEA

CEA is used to compare conservation strategies that have effects of different magnitudes. In a CEA, the strategy's effect is divided by its cost and gives priority to those strategies with the greatest biological effect relative to its economic cost. A CEA can be used as a decision tool to rank strategies for implementation until a budget is exhausted. A related decision beyond this paper's scope considers how to allocate resources within a given strategy, for example, what proportion of funds should be allocated to each nesting beach. Generally, CEA tests the null hypothesis that the mean cost-effectiveness of one strategy does not differ from that of a competing strategy.

We illustrate the least-cost solution to achieving population level E as a reduction in mortality on nesting beaches of X_2^* and on foraging grounds of X_1^* (Fig. 1). Suppose current projects reduce mortality on foraging grounds to X_1' and reduce mortality on nesting beaches to X_2' for a total cost (TC'). One could achieve the same population level by investing more in projects to reduce mortality on nesting beaches (to X_2^*) and investing less in projects to reduce mortality on foraging grounds (to X_1^*). This achieves the same population level, E , at a lower cost, TC^* .

In economic terms, efficiency occurs when resources (inputs) are used in such a way as to produce the maximum possible output. When alternative projects are not mutually exclusive and may be combined at various levels, efficiency requires that each project be implemented to the level at which the last dollar invested in each project returns the same benefit, where the benefit in

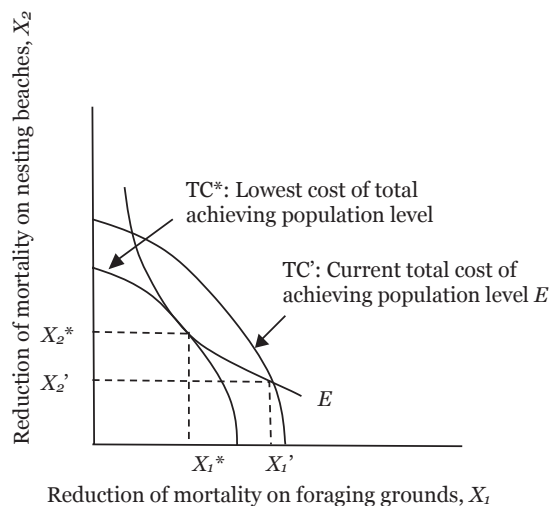


Figure 1. Costs of reduction of mortality of Pacific leatherback turtles on nesting beaches relative to foraging grounds to achieve a given population level (E).

this case is the marginal reduction in turtle mortality. It is assumed that marginal returns decrease as investment in a project increases. If the marginal benefit of one project is much higher than another, additional funds should keep being allocated to that project until the marginal benefits of the projects equalize. When projects cannot be implemented at continuously varying scales or there are greater than proportional benefits from increasing the scale of competing projects, a discrete choice of one project over another may be required.

Data and Uncertainty

Conservation projects involve a range of activities that incur costs. Some of these may involve one-time expenditures, whereas others may be recurrent. In 2005, we collected data on the costs of 3 leatherback conservation projects. For some projects, we estimated costs from available data, such as fishery cost-earnings studies or annual reports. To measure the benefits of the conservation projects, we developed a population model (and a biological metric).

Because there are still few data with which to estimate population models' basic life-history parameters for leatherback turtles, the population trajectory even without conservation investments is uncertain. Quantitative analyses are often based on population viability analyses (PVA) that use trends in the number of adult female turtles in a population (often computed from the number of observed nests). These approaches require information on basic life-history parameters (e.g., survival rates, age at first reproduction, and fertility). It is a common

practice to include uncertainty in estimated life-history parameters for PVA (e.g., Caswell 2001).

Because marine turtles are long-lived species, natural survival rates are constrained. Fecundity is perhaps one of the least uncertain parameters to quantify for sea turtles because it is based on reproductive output of females derived from egg counts; these data are routinely recorded at nesting beaches. In contrast, age at first reproduction is a difficult parameter to estimate because it has generally not been possible to mark hatchlings and follow them to maturity or directly determine age in sea turtles from empirical observation. Demographic model outputs are more sensitive to the effects of uncertainty in age at maturity (or age at first reproduction) than those from other parameters.

Other than a few studies (e.g., Limpus et al. 1994) in which hatchling loggerhead cohorts were followed to their maturity, age at first reproduction is estimated indirectly through skeletochronology (e.g., Avens et al. 2009) or inferred from observed population growth rates (e.g., Dutton et al. 2005), with controversial outcomes. Age at first reproduction affects adult survival and fertility. Consequently, accurate and precise estimates of age at maturity, which may vary from population to population depending on the productivity of the environment, is important for developing effective conservation and management rules.

To compare the strategies' effects, we converted the estimated number of leatherback hatchlings from a nesting beach to a measure comparable with turtle captures avoided in bycatch reduction projects. For simplicity, we used stage-specific reproductive values (RVs) to provide an estimate of female adult equivalence. Wallace et al. (2008) suggest using RVs as a metric to develop conservation strategies. We used an RV of 426 for adults (RV for hatchlings is 1), which we based on rough estimates of life-history parameters (T. Eguchi, unpublished data).

Different approaches are used to address uncertainty in marine resource management (Regan et al. 2005). The traditional approach is to parameterize a model with best estimates of parameters and then conduct a sensitivity analysis. This is the approach taken in Gjertsen (2011), where the authors used best estimates of parameters to analyze cost and benefit data to make preliminary cost-effectiveness comparisons. The most common method of directly incorporating uncertainty in parameter estimates is to assign a probability distribution to the parameter in question with an assumed mean and standard deviation (Halpern et al. 2006). We used this method here. We directly incorporated uncertainty regarding estimates by providing probability distributions for the model parameters and conducting Monte Carlo simulations of the model. We implicitly assumed technical efficiency (i.e., within a project the given effect cannot be achieved at a lower cost). We implicitly assumed that the marginal

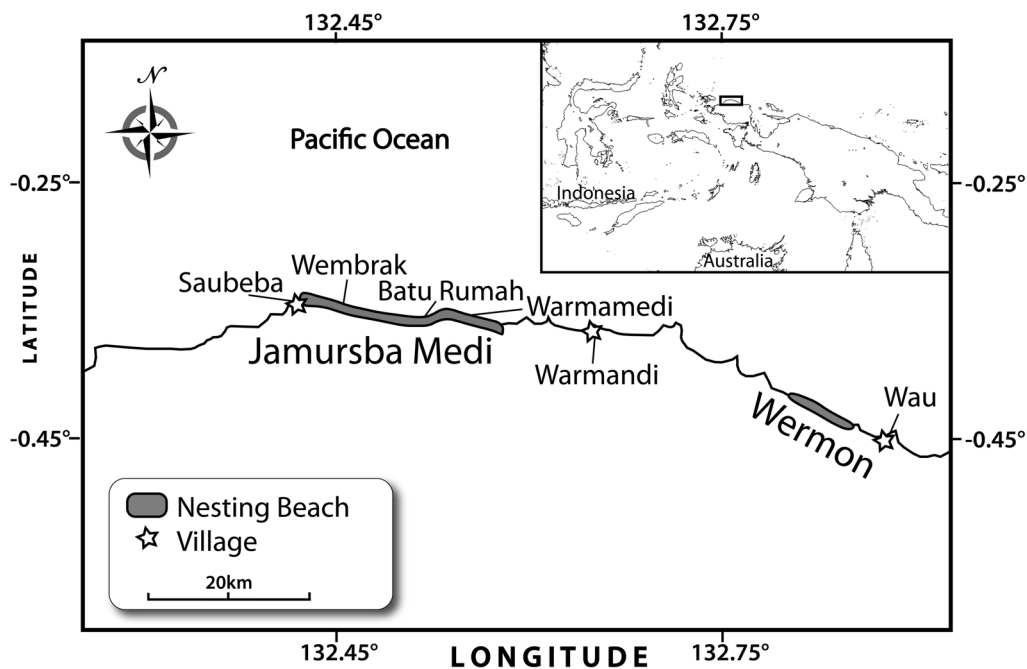


Figure 2. Map of leatherback turtle nesting sites in Jamursba Medi and Wermon, Papua, Indonesia (Tapilatu et al. 2013).

cost of reducing turtle mortality is constant, although we expect it to increase over some period; as turtle mortality progressively declines, costs per unit reduction will rise.

Description of Strategies and Measurement of Costs and Benefits

JAMURSBBA MEDI AND WERMON NESTING BEACHES

Jamursba Medi and Wermon beaches in Papua, Indonesia, host the largest remaining leatherback nesting population in the Pacific, and together approximately 75% of nesting in the western Pacific occurs on these beaches (Dutton et al. 2007). On the 2 beaches, 5000–6000 nests/year are created (Hitipeuw et al. 2007). Jamursba Medi is a series of 3 beaches covering a 20-km stretch on the northern coast of Bird's Head peninsula in Papua Barat, Indonesia (formerly Irian Jaya), which is 130 km northeast of the nearest town, Sorong (Fig. 2). Wermon beach is approximately 30 km east of Jamursba Medi and extends for 6 km (west of Manokwari).

On both beaches egg consumption by humans was high until a conservation project was started in Jamursba Medi in 1993 and in Wermon in 2003 by WWF-Indonesia. This organization has been working with the communities, Balai Besar Konservasi Sumber Daya Alam (BKSDA)-Sorong, and Papua State University (UNIPA) to protect nesting leatherbacks, and human consumption of eggs has essentially ceased. Community members are hired as monitors to collect data and protect nests from predators.

Since we collected data for this paper, UNIPA began leading the conservation and monitoring project. Because the nesting beaches are far from large human settlements and there were no roads or electricity in the village, WWF built a base camp on the beach for their staff and the patrol team on Jamursba Medi beach. This camp included a few basic structures with a generator and water pump.

Cost data from a number of other nesting beach projects throughout the western Pacific indicated conservation projects on nesting beaches have relatively high fixed costs (costs that are not easily altered in the short run or with the scale of the operation) at each site but low variable costs (costs that can be modified in the short run or as the scale of the operation changes). A site with 3000 nests has protection costs similar to a site with 30 nests, mainly because a large portion of administrative costs (e.g., rent, utilities) and field costs (e.g., transportation) is not particularly sensitive to the size or scale of the project. This tends to confer economies of scale to larger sites because the fixed costs are spread out over a larger number of nests and hatchlings. Additional nests can be protected quite cheaply (e.g., by hiring additional patrollers at relatively low wages), although this will vary by location. Variable costs are mainly patroller wages and field equipment. These costs represent a small portion of overall expenditures (20–50%) and increase slowly as nesting site size increases. To a certain extent, additional beach area can be covered at little marginal cost, that is, until the area becomes so great that some of the costs need to be replicated (e.g., meetings and training with additional communities, additional field stations). There are

Table 1. Variables related to costs and benefits of protecting nesting beaches in Jamursba Medi and Wermon, Indonesia.^a

<i>Cost^b</i>		<i>Benefit</i>	
<i>variable description</i>	<i>distribution</i>	<i>variable description</i>	<i>distribution</i>
Capital assets Jamursba Medi, <i>A</i> (\$)	uniform (13,130; 27,280)	fraction of female hatchlings, <i>A</i>	triangular (0.53; 0.6; 0.65)
Capital assets Wermon, <i>B</i> (\$)	best estimate (11,920)	number of nests Wermon, <i>B</i>	best estimate (2,520)
Economic life, <i>C</i> (years)	triangular (5;10;20)	number of nests Jamursba Medi, <i>C</i>	best estimate (3,720)
Administrative costs, <i>D</i> (\$)	best estimate (75,693)	nests destroyed per year, <i>D</i>	beta (2.7; 15.4)
Field costs, <i>E</i> (\$)	best estimate (72,269)	nest depredated per year, <i>E</i>	beta (2.9; 10.4)
Annual egg revenue/site, <i>F</i> (\$)	uniform (23,037; 76,996)	number of eggs/nest, <i>F</i>	gamma (120; 0.62)
Transfers, <i>G</i> (\$)	best estimate (42,655)	hatchling success rate Wermon, <i>G</i> (fraction/year)	beta (1.64; 1.84)
		hatchling success rate Jamursba Medi, <i>H</i> (fraction/year)	triangular (0; 0; 1)
		adult reproductive value, <i>I^c</i>	gamma (10.225; 42.679)

^aAdditional information about estimates is in Supporting Information.

^bMonetary unit (\$) is value of US\$ in 2005.

^cRelative contribution of adults to current and future reproduction compared with the contribution of hatchlings.

also economies of scope through which other sea turtle species are protected at the same site, but for simplicity's sake we did not consider these additional effects.

We estimated annual values of different cost components of the nesting beach projects as described by

$$[(A + B)/C] + D + E + (F - G). \quad (1)$$

Table 1 contains definitions of these variables. The nesting project's annual economic costs were approximately \$209,261, which included annual administrative costs, field costs, capital asset expenditures, and foregone community egg revenue minus transfers (i.e., scholarships, boats, and local wages provided by WWF) (Gjertsen 2011). Because of the remote location of this nesting beach, foregone development opportunities due to turtle conservation were not relevant. However, foregone development could become an issue in the future, for example, if current mineral prospecting results in commercial interest in the area or if tourism infrastructure is developed.

To describe the benefits of the nesting beach project in terms of adult females, we estimated the annual number of female hatchlings and normalized it by the adult RV as described by

$$\{[A \times B \times [1 - (D + E)] \times F \times G]/I\} + \{[A \times C \times [1 - (D + E)] \times F \times H]/I\}. \quad (2)$$

The components of Eq. (2) are as follows:

{(percentage of female hatchlings) × (no. of nests) × [1 - (nest destruction rate + nest predation rate)] × (no. of eggs/nest) × (hatching success rate)}/adult RV. Table 1 contains definitions of these variables. The value

of hatchlings, measured by this formula in Gjertsen (2011), is approximately 134 adult females/year.

HAWAIIAN SHALLOW-SET LONGLINE FISHERY REGULATIONS

Leatherbacks from the population nesting in Papua, Indonesia, are taken as bycatch in areas fished by the HLL fishery (Dutton et al. 2000; Benson et al. 2011). After a 3-year closure due to unacceptable levels of leatherback and loggerhead bycatch, the HLL fishery reopened in 2004 under a set of stringent regulations designed to reduce bycatch. The main changes were reduction in annual set numbers (reduced by approximately 50%); enactment of annual maximum limits on sea turtle bycatch (16 leatherbacks, 17 loggerheads; if limits are reached, the fishery is closed for the remainder of the calendar year); required use of 18/0 or larger circle hooks (no smaller than 50 mm [1.97 inches] outer diameter) with 10° offset; and required use of mackerel-type bait.

We estimated the annual economic costs of the HLL fishery regulations as the direct and indirect or opportunity costs (Table 2). Opportunity costs are the foregone net benefits from the next-best alternative; thus, costs are the observer costs and expected annual revenue loss from the regulations, that is

$$\text{triangular}[0, (B \times C), (B \times D)] + E. \quad (3)$$

Gjertsen (2011) estimated the annual economic costs from the HLL regulations as \$2,805,426 on the basis of expected annual revenue loss from the regulations plus the observer costs: $(B \times C) + E$.

Table 2. Variables related to costs and benefits of Hawaiian shallow-set longline fishery regulations.^a

<i>Cost^b</i>		<i>Benefit</i>	
<i>variable description</i>	<i>distribution</i>	<i>variable description</i>	<i>distribution</i>
Expected annual revenue loss after regulations, <i>A</i> (\$)	triangular (0; <i>BC</i> ; <i>BD</i>)	preregulation annual turtle take per 1000 hooks, <i>A</i>	best estimate (0.029)
Preregulation revenue, <i>B</i> (\$)	best estimate (54,385,150)	preregulation annual number of hooks, <i>B</i> (in 000s)	triangular (2000; 4000; 4000)
Expected reduction in revenue, <i>C</i> (low value)	best estimate (0.0225)	preregulation annual mortality rate, <i>C</i>	triangular (0; 0.14; 1)
Expected reduction in revenue, <i>D</i> (high value)	best estimate (0.044)	postregulation annual maximum allowable turtle take, <i>D</i>	best estimate (16)
Observer cost, <i>E</i> (\$)	best estimate (1,581,760)	postregulation annual turtle take per 1000 hooks, <i>E</i>	best estimate (0.005)
		postregulation annual number of hooks, <i>F</i> (in 000s)	triangular (1000; 2000; 2000)
		postregulation annual mortality rate, <i>G</i>	triangular (0; 0.13; 1)

^aAdditional information about estimates in Supporting Information.

^bMonetary unit (\$) is value of US\$ in 2005.

We estimated the benefits from the HLL fishery regulations as a reduction in expected annual mortality (Table 2):

$$(A \times B \times C) - \min[(D, (E \times F \times G))]. \quad (4)$$

Benefits from the HLL regulations in Gjertsen (2011) were a reduction in mortality by 100 adult female leatherbacks: $[(A \times B \times C) - D]$.

CDGN TEMPORAL AND AREA CLOSURES

We estimated the costs of the CDGN temporal and area closures as the direct and indirect cost (i.e., observer cost plus short-term economic profit per set multiplied by the foregone sets because of the closure) (Table 3):

$$(A \times E) + F. \quad (5)$$

Gjertsen (2011) estimated the cost from the CDGN closures as \$2,053,964/year.

We estimated the benefits of the CDGN closures as a reduction in expected annual mortality due to the closure. This was measured as the reduction in expected annual take postclosure compared with preclosure multiplied by the mortality rate (Table 3):

$$(A - J) \times K, \quad (6)$$

where we used the following equations: leatherback take preclosure (minimum) = $[(B + C)/(D \times E)]$; leatherback take preclosure (maximum) = $H \times I$; leatherback take postclosure (minimum) = 0; and leatherback take postclosure (maximum) = $[(F \times C)/G]$. Gjertsen (2011) estimated the benefits from the CDGN fishery closures as a reduction in mortality by 10 adult female leatherbacks $[(A - J) \times K]$.

We did not estimate the full extent of regulatory costs for the Hawaiian and California interventions because a complete estimate would include unavailable information on staff time and meeting time allocated specifically to program administration. Observer program costs are broad estimates and are not solely for the purpose of leatherback conservation and may therefore be overestimated.

We conducted Monte Carlo simulations of the model (Eqs. 1–6) in @Risk (version 6, Palisade, Ithaca, New York). We performed 5000 iterations with Monte Carlo sampling.

Results

Analysis conducted in Gjertsen (2011) revealed that current activities producing hatchlings at Jamursba Medi and Wermon nesting beaches cost more than 10 times less per adult female turtle than the HLL regulations and more than 100 times less per adult female turtle than the CDGN temporal and area closures (Table 4). For the same cost, the nesting beach project thus yielded over 10 times as many adult female leatherbacks as HLL regulations and over 100 times as many adult female leatherbacks as the temporal and area closure.

When we conducted simulations as described by Eqs. 1–6, the median cost per adult female turtle through nesting beach protection was \$1,132 (SD 1,404). The median cost per adult female turtle through HLL regulations was \$90,118 (SD 1,537,263). The median cost per adult female turtle through the CDGN closures was \$171,000 (SD 85,690).

These results were quite robust to uncertainty surrounding parameter estimates. Most cost-effectiveness

Table 3. Variables related to costs and benefits of California drift gillnet time-area closure.^a

<i>Cost^b</i>		<i>Benefit</i>	
<i>variable description</i>	<i>distribution</i>	<i>variable description</i>	<i>distribution</i>
Number of annual sets, <i>A</i>	triangular (418; 836; 1273)	annual leatherback take preclosure, <i>A</i>	triangular (8.7; 8.7; 48.2)
Average annual number of sets in closed area before closure, <i>B</i>	best estimate (836)	total observed takes inside closed area preclosure, <i>B</i>	best estimate (18)
Reduction in total annual sets after closure, <i>C</i>	best estimate (1273)	total observed takes outside closed area preclosure, <i>C</i>	best estimate (5)
Half of average annual number of sets in closed area before closure, <i>D</i>	best estimate (418)	annual observer coverage rate, <i>D</i>	best estimate (0.2)
Short-term economic profit per set, <i>E</i> (\$)	best estimate (1799)	number of years observed, <i>E</i>	best estimate (11)
Annual observer costs, <i>F</i> (\$)	best estimate (550,000)	annual number of sets outside closure post closure, <i>F</i>	best estimate (1448)
		annual number of observed sets outside closed area preclosure, <i>G</i>	best estimate (4147)
		highest annual observed turtle takes per set preclosure, <i>H</i>	best estimate (0.018)
		average number of total sets preclosure, <i>I</i>	best estimate (2,716)
		annual leatherback take postclosure, <i>J</i>	triangular (0; 1.7; 1.7)
		annual mortality rate, <i>K</i>	uniform (0.54; 0.63)

^aAdditional information about estimates in Supporting Information.

^bMonetary unit (\$) is value of US\$ in 2005.

Table 4. Annual cost per adult female of leatherback protection strategies.

	<i>Annual cost (2005 US\$)</i>	<i>Ratio of cost of fisheries interventions relative to nesting beach intervention (2005 US\$)</i>
Jamursba Medi and Wermon nesting beach	1558	1558/1558 = 1
Hawaiian shallow-set longline fishery	28,054	28054/1558 = 18
California drift gillnet fishery	205,396	205396/1558 = 132

simulation results for nesting beach protection relative to HLL regulations showed that it was tens of thousands to hundreds of thousands of dollars cheaper per adult turtle to protect beaches than it was to have HLL regulations (mean [SD] = 148,390 [1,537,261]). The range was considerable, from nesting beach protection costing \$46 million less than HLL regulations to nesting beach protection costing \$48 million more than the HLL regulations, but nearly all 5000 data points clustered about the mean. There was a <1% chance of HLL fishery regulations being more cost-effective than nesting beach protection.

The results were most sensitive to the number of eggs per nest, the expected annual revenue loss from regulations, and number of hooks before regulations.

The bulk of our simulation results for cost-effectiveness of nesting beach protection versus CDGN closures indicated that it was hundreds of thousands of dollars cheaper per adult turtle to protect nesting beaches than to have CDGN closures (mean [SD] = 188,672 [85,677]) (Fig. 3). There was a 0% chance of CDGN closure being more cost-effective than nesting beach protection. The results were most sensitive to leatherback take preclosure, followed by foregone sets due to closure, mortality rate, leatherback take postclosure, and reduction in expected annual mortality.

Discussion

Conservation investments in nesting beach protection and bycatch mitigation activities can target different stages in a species' life cycle in a holistic conservation strategy. Because all stages of the life cycle are important for population persistence, interventions targeting each stage represent a necessary but not sufficient condition for conservation and population recovery and requires an allocation of conservation resources.

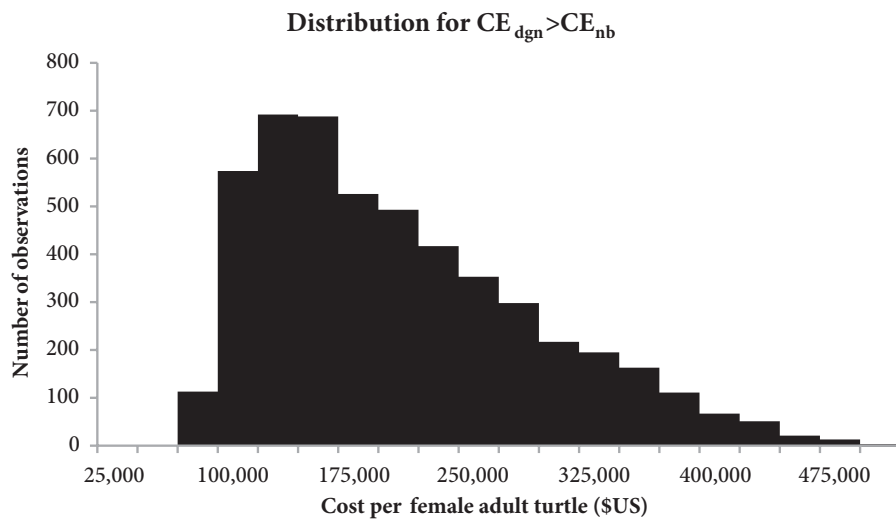


Figure 3. Distribution of cost per adult female turtle of protecting nesting beaches (CE_{nb}) in Papua, Indonesia, versus cost per adult female of temporal and area closures of the California drift gillnet fishery (CE_{dgn}) ($CE_{dgn} - CE_{nb}$).

In the case of the leatherback turtle, interventions to protect turtles, especially females, yield greater positive reproductive effect for a population than enhancing egg production because of the long lives and fecundity of sexually mature females and relatively low survival of eggs and hatchlings. Nonetheless, conservation activities with the highest biological effect may also be the most costly, so with a finite budget, undertaking these activities may result in a lower total effect than more of the less costly, lower impact activity. Under current conditions, we found that nesting site conservation to rebuild Pacific leatherback populations was the most cost-effective investment. Hatchling production in the western Pacific is greatest on Jamursba Medi and Wernon beaches. Thus, these beaches represent one of the better-case scenarios for cost-effective nesting beach conservation. Limits as to how much can be achieved by investing in nesting beach protection suggest that at some point the effect per dollar will decrease. These diminishing returns apply to conservation dollars allocated to any specific conservation activity, but given the orders-of-magnitude difference in cost-effectiveness, expanding nesting beach protection should dominate over any reasonable range of conservation investments in the near future. Low hatching success at many nesting beaches indicates substantial expected gains from increasing investment in improving hatchling production at these sites (Tiwari et al. 2011). In addition, the establishment of community-based nesting conservation projects and presence of patrollers have an added benefit of providing protection for nesting females at little or no additional cost.

The 2 at-sea regulations represent relatively high-cost, low-impact strategies. There may be more cost-effective bycatch reduction strategies, such as fisheries closures off nesting beaches during nesting season (Yeo et al. 2011). Such low-cost, high-impact opportunities should be pursued, for example, reducing bycatch when there is

a small number of fishers that cause high levels of bycatch (Peckham et al. 2007; Yeo et al. 2011).

Results for the CDGN temporal and area closures and the HLL regulations indicated leatherback protection on fishing grounds can be costly, mainly due to the opportunity cost of foregone profits from a decrease in effort or catch, and the effects of these measures are highly variable. However, the fact that other species and their habitats are protected by closures increases net benefits. Technological fixes, such as lower impact fishing gear, generally entail lower economic costs than temporal and area closures, which often close the most productive and profitable fishing grounds. Although substituting circle for J hooks in the pelagic longline fishery for swordfish was effective and did not reduce catch rates (Watson et al. 2005), finding a comparable bycatch-reducing technology for drift gill nets and other net fisheries has been more challenging.

Because leatherbacks are migratory, bycatch-reduction strategies are a weakest link technology. Effects may be zero (or negative) if efforts are only implemented in one area or one fishery, particularly when there is the possibility of imports from unregulated fisheries filling the swordfish harvesting shortfall (called production and trade leakages) and transfer of turtle mortality to unregulated fisheries. Because any one country's outcome depends not only on its own actions, but also on the actions of others, unilateral actions are unlikely to be successful, and self-enforcing multilateral conservation cooperation or coordination is instead required.

Cost-effectiveness of conservation of sea turtle nesting sites can be orders of magnitude greater than at-sea conservation, even when accounting for uncertainty in the main variables. These results reinforce the call for industry and developed nations to mitigate fishery bycatch by financing nesting site protection (Steering Committee of the Bellagio Conference on Sea Turtles 2004). This mitigation cannot offset fisheries bycatch for rare species until

these populations rebuild (Finkelstein et al. 2008; Dutton & Squires 2011; Dutton et al. 2011), and for other reasons such mitigation must include benefits to communities at nesting sites that exceed their conservation opportunity costs and avoid adverse selection of mitigating what would have been done anyway (Janisse et al. 2010). Starting in 2004, the CDGN fleet pioneered noncompensatory mitigation for Mexican nesting sites financed by a voluntary lump-sum tax (Janisse et al. 2010). Similarly, U.S. tuna canners, through the International Seafood Sustainability Foundation, voluntarily mitigate global longline catches through noncompensatory, global, nesting site conservation financed by an ad valorem tax on tunas. The first dividend of these double-dividend Pigovian taxes is the tax that partially internalizes sea turtle mortality external cost and creates incentives that more closely align swordfish producer and consumer behavior with social and conservation objectives. The second dividend is conservation benefits financed by tax receipts. Voluntary policies can be successful under some conditions, but there are limits, and complementary policies may be necessary (Segerson 2010).

Sea turtle nesting site conservation also may have advantages in terms of tractability compared with the difficulties of addressing stochastic bycatch of small-scale and artisanal fisheries and relatively rare species (Peckham et al. 2007; Segerson 2011) and the multilateral cooperation necessary for reducing bycatch in a transboundary fishery. Leatherbacks pass through the high seas, different exclusive economic zones, convention areas of 2 Pacific regional fishery management organizations, and several other smaller subregional territories. Because of their terrestrial nesting habitat and highly migratory aquatic life history, transboundary leatherbacks are thus subject to transnational externalities. In contrast to the aquatic habitat, nesting habitat occurs at a limited number of sites. There is a wide range of nesting site conservation strategies, including strategies that incorporate social norms and economic incentives (Dutton et al. 2011; Dutton & Squires 2011; Gjertsen & Stevenson 2011), but this discussion extends beyond the scope of this paper.

Our results suggest that additional investment in nesting site conservation at the margin can enhance cost-effective Pacific leatherback conservation as part of a holistic strategy that reduces threats at all life stages.

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HLL fishery. The authors are responsible for remaining errors.

Supporting Information

Description of variables related to costs and benefits (Appendix S1), estimates of costs and benefits (Appendix S2), summary statistics from the simulations on distribution of benefits and costs (Appendix S3), and graphical results of the simulations on distribution of cost per adult female turtle (Appendix S4) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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