Density-dependent habitat selection and the modeling of sperm whale (*Physeter macrocephalus*) exploitation

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Abstract: The monitoring and management of sperm whale (*Physeter macrocephalus*) populations have proved problematic. Studies of living animals indicate that movements are largely determined by resource availability, thus suggesting that density-dependent habitat selection may be a realistic framework within which to study sperm whale populations. A model, in which animals migrate between 2 × 2° squares at rates that depend on relative resource availability, was used to examine the effects of whaling on measures of sperm whale abundance. The model simulated four types of whaling: shore-based whaling, pelagic open-boat whaling by many boats, pelagic whaling by a fleet based around one factory ship, and pelagic whaling by a fleet sequentially exploiting different parts of the study area. Catch per unit effort was found to have little relationship with population size in any part of the study area for shore-based whaling and for pelagic whaling when the study area was sequentially exploited. Thus, in these circumstances, catch per unit effort should not be used as a measure of depletion. To give a reasonable assessment of depletion, visual or acoustic surveys must extend well beyond the areas being exploited.

Résumé : La surveillance et la gestion des populations de cachalots macrocéphales (*Physeter macrocephalus*) se sont avérées problématiques. Les études sur les animaux vivants montrent que leurs déplacements sont largement déterminés par les ressources disponibles, ce qui laisse penser qu'il serait réaliste d'étudier les populations de cachalots macrocéphales en fonction d'une sélection de l'habitat dépendante de la densité. On a utilisé un modèle dans lequel les animaux migrent entre des carrés de 2° × 2° à des rythmes qui dépendent des ressources disponibles pour examiner les effets de la chasse sur les mesures de l'abondance des cachalots macrocéphales. Le modèle simulait quatre types de chasse : chasse depuis le rivage, chasse pélagique réalisée par de nombreux bateaux non pontés, chasse pélagique réalisée par une flottille rattachée à un bateau-usine, et chasse pélagique réalisée par une flottille exploitant séquentiellement différentes zones de l'aire de l'étude. On a observé que les captures par unité d'effort étaient peu reliées à la taille de la population partout dans l'aire de l'étude dans les cas de la chasse depuis le rivage et de la chasse pélagique séquentielle. Ainsi, dans ces conditions, les captures par unité d'effort ne devraient pas être utilisées comme mesure de la déplétion des populations. Pour obtenir une évaluation raisonnable de cette déplétion, on devrait effectuer des relevés visuels ou acoustiques s'étendant bien au-delà des zones exploitées.

[Traduit par la Rédaction]

Introduction

During the 1970s and early 1980s the Scientific Committee of the International Whaling Commission made considerable efforts to model sperm whale (*Physeter macrocephalus*) populations with the intention of better managing exploitation (e.g., International Whaling Commission 1980). The application of the methods that were developed have problems for a number of reasons, which include uncertainties about natural history parameters (Best et al. 1984), misreporting of data (Zemsky et al. 1995), the effects of adult sex ratio and social structure (Botkin et al. 1980), as well as fundamental issues concerned with assessment mechanisms (Cooke 1986).

One of the most controversial and difficult issues that the Scientific Committee of the International Whaling Commission faced during these assessments concerned stock bound-

aries (Donovan 1991). There is evidence from artificial and natural marking studies that, while some sperm whales may be resighted within a small area after intervals of months or years, others can move 1000 km or more (Kasuya and Miyashita 1988; Dufault and Whitehead 1995). A review of studies of sperm whale stock structure, including recent genetic work, suggested that there are no clear stock divisions, defined by lines that animals rarely cross, for sperm whales in the world's oceans (Dufault et al. 1999). Thus, a model of sperm whale populations based on discrete stocks is likely to be fundamentally invalid.

Recent research has examined the movement patterns of living animals. It seems that the movements of groups of female sperm whales are related to feeding success. When feeding success is high, groups zigzag back and forth over areas a few tens of kilometres across, whereas when success is low, they move in straight lines at speeds of about 100 km/day (Whitehead 1996; Jaquet and Whitehead 1999). This means that, within areas a few tens or hundreds of kilometres across, residence times are long when feeding success is high and short when it is low (Whitehead 1996).

Such movement patterns can lead to a system of density-

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dependent habitat selection in which animals tend to distribute themselves geographically so that feeding success is roughly equal everywhere (MacCall 1990). Whitehead et al. (1997) have suggested that density-dependent habitat selection may explain a decline in the number of sperm whales off the Galápagos as animals redistributed themselves following the end of intense whaling off Peru.

In this paper, I explore how density-dependent habitat selection and whaling might interact for sperm whales and the implications for the management of populations. I use a simulation model in which whales move between ocean areas depending on relative resource availability and then allow the population to be exploited in a variety of ways (as suggested by Hilborn and Walters (1987) and MacCall (1990)). I then examine how catch per unit effort (CPUE) is related to population size. The model used is simplistic, but parameters are chosen to approximate reality.

Methods

Model of density-dependent habitat selection for sperm whales

A simple model of density-dependent habitat selection of sperm whales was constructed (using Matlab 5.2) with the following characteristics.

(i) Two-dimensional array of squares indexed by i ($i = 1,..., I$) (a one-dimensional index is used to simplify the notation). Each has a population of whales, n_i, that varies with time, and a resource availability, r_i, that, in some versions, varies with time.

(ii) Movement of whales between squares. Each square has at most four surrounding squares. Transition probabilities from square i to square j at the start of each time unit, $P(i,j)$, are given by

$$P(i,j) = abn_i r_j^2 / [(r_i^2 + bn_i)(r_j^2 + bn_j)]$$ if i and j are neighbouring squares

$$P(i,j) = 0$$ if i and j are not neighbouring squares

$$P(i,j) = 1 - \sum_{j \neq i} P(i, j),$$

where a and b are constants with $0 < a \leq 0.25$ and $b > 0$. Constant a can be interpreted as the overall rate of migration during a time period, and constant b as expressing the relative importance of resource abundance per animal in the source (high b) and receiving squares (low b) in determining migration rates. Constant b should have a value comparable with the n values. This expression was chosen as it has the following properties (when i and j are neighbouring squares): $P(i,j) \geq 0$; $n_i P(i,j)$ increases as r_i/n_i decreases: more emigration with less resource per animal in source square; $n_i P(i,j)$ decreases as r_j/n_j decreases: less emigration with less resource per animal in receiving square; $\Sigma P(i,j) \leq 1$ (with summation over all neighbouring squares j for each i): total emigration from a square is less than the number of animals in it; and $n_i P(i,j) = n_j P(j,i)$ when $r_i/n_i = r_j/n_j$: no net migration between neighbouring squares when resource per animal is equal in them. Although there are other expressions that satisfy these conditions, they are restrictive. This migration model is illustrated in Fig. 1.

(iii) Whaling. Animals are then removed from square i as follows in each time unit, so that

$$n_i(t + 1) = \left[\sum_{j=1,...,I} n_j(t) P(j,i) \right] s_i(t + 1),$$

where $s_i(t)$ is the selectivity in square i at time t.

Fig. 1. Illustration of the density-dependent movement model. Initial whale numbers and resource availabilities over four adjacent squares illustrated in the upper diagram trigger movements of whales between squares (centre diagram), and thus a distribution of whales one time unit later shown in the lower diagram. Note that the proportion of whales moving to an adjacent square depends on the relative resource availabilities, per whale, in the two squares.
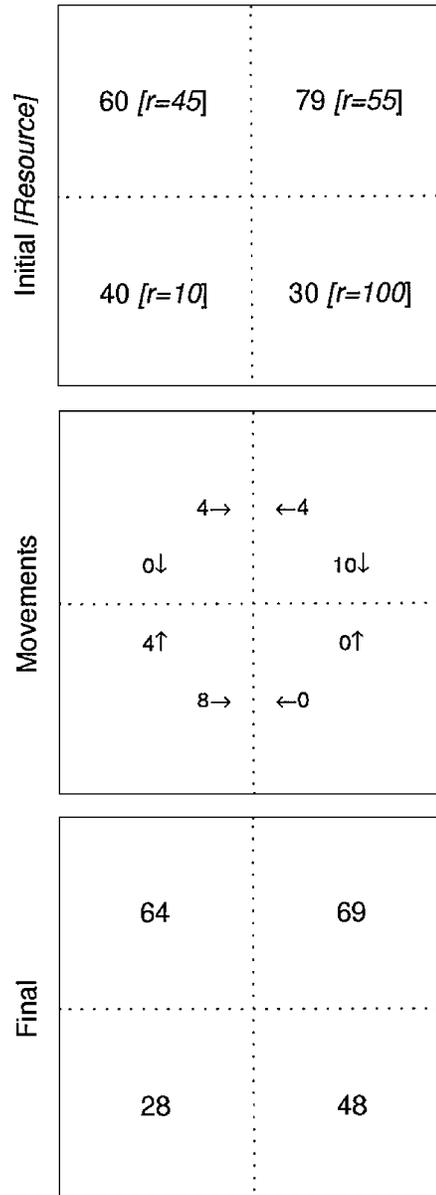
Parameterization of model

The form and parameters of the model were chosen to roughly approximate what is known about the biology of the female and immature sperm whales in the eastern tropical Pacific Ocean. In this area, there is little evidence for seasonal or breeding migrations by females and immatures (e.g., Hope and Whitehead 1991). No attempt has been made to incorporate the migrations of adult males into, and out of, the study area, as these animals constitute only a few percent of the population (Hope and Whitehead 1991) and little is known of their migrations.

Fig. 2. Initial distribution of resource availability, and sperm whales, in 2° squares of the eastern tropical Pacific from the charts of Townsend (1935). Darker shading indicates more resources and more animals. The white squares on the eastern side of the map represent the South and Central American mainland and are not considered in the simulations.
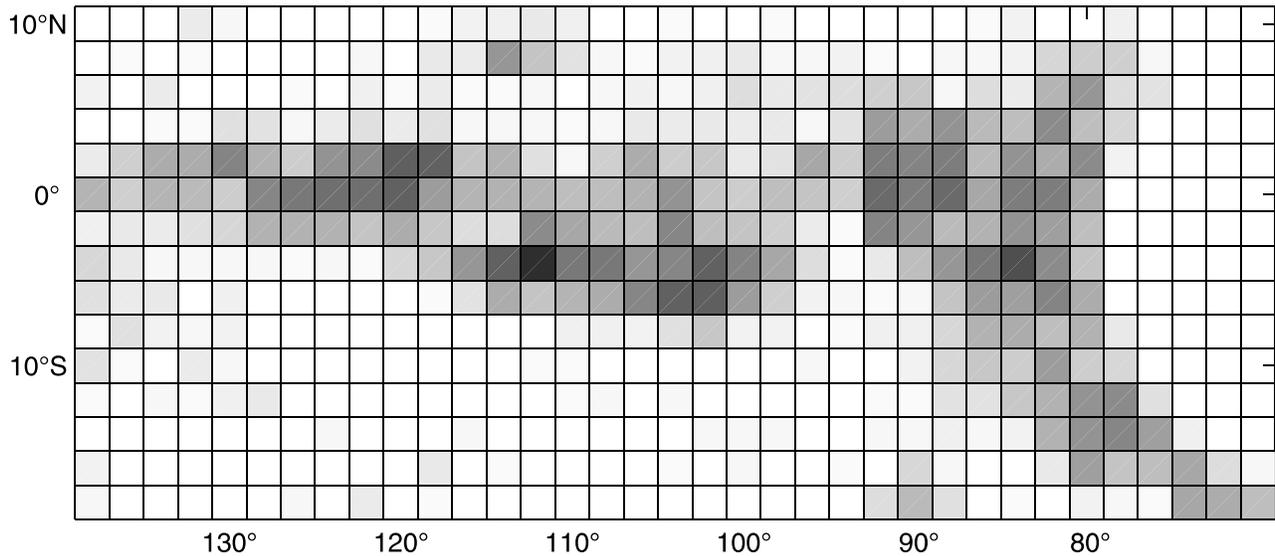

Table 1. Estimated initial population sizes from the x-intercept of the linear regression of CPUE on cumulative catch during the first and second decades of whaling for four types of whaling and two implementations of resource availability (results for two runs with temporally variable resources are separated by a solidus).

| | Resource availability | | | |
| | Temporally constant | | Temporally variable | |
Type of whaling	First decade	Second decade	First decade	Second decade
Shore based	17 730	25 501	15 101/14 470	22 938/23 061
Pelagic, open boat	49 950	49 950	49 950/49 950	49 950/49 950
Pelagic, factory fleet	38 539	43 932	40 443/39 801	43 808/43 352
Pelagic, sequential exploitation	42 548	–287 758	50 035/53 801	–36 032/–16 635 657

Note: The true initial population size was 50 000 animals.

Time units were weeks, and the simulations were run over 19.2 years (1000 time units). The study area is the eastern tropical Pacific bounded by 20°S, 11°N, 79°W, and 140°W. The study area was divided into 2° latitude × 2° longitude squares. Land areas within the study area were not considered, leaving 472 squares.

The initial resource availability in a square, $r_i(0)$, was proportional to the number of plots of sperm whale kills in that square in the maps of Townsend (1935), as tabulated by Jaquet et al. (1996) plus 0.5. The total resource availability over the study area was 50 000. Two implementations were considered: (*i*) temporally constant resource availability and (*ii*) temporally variable resource availability, with some spatial and temporal autocorrelation, so that a measure of the relative resource availability in square i at time t is given by

$$q_i(0) = 0.1z_i(0)$$

$$q_i(t) = 0.95[6q_i(t-1) + \Sigma q_j(t-1)]/(6 + m_i)$$

$$+ 0.05z_i(t)$$

where the summation is over all neighbouring squares j, m_i is the number of neighbouring squares of square i, and z is a normal random variable with mean 0 and variance 1. From these q_is, the absolute resource availability in square i at time t was calculated from

$$r_i(t) = r_i(0)\exp[12q_i(t)].$$

This produces $r_i(t)$ with a geometric mean equal to $r_i(0)$. The parameters and form of this model were chosen so that the mean CV for each square (0.95) and mean autocorrelation between adjacent weeks (0.57), respectively, equaled the estimated CV and autocorrelation between weekly defecation rates, a measure of feeding success, measured from sperm whales off the Galápagos Islands (data from Whitehead 1996). As in the data on defecation rates, the resource trajectories produced by this model showed increasing variance over time scales up to about 6 months.

The initial populations in each square ($n_i(0)$) equaled the initial resource availability ($r_i(0)$), as indicated in Fig. 2, and both are based on the distribution of sperm whale kills plotted by Townsend (1935). Thus, the total initial population of sperm whales in the area equaled 50 000 animals. This follows the suggestion that the density of plots on Townsend's (1935) charts likely correlates well with prewhaling sperm whale distributions (Whitehead and Jaquet 1996) and is roughly consistent with Wade and Gerrodette's (1993) census estimate of 22 700 sperm whales in the eastern tropical Pacific, given that they made no correction for whales being underwater and so invisible during their surveys.

In the movement model, parameter a was set at 0.25, indicating that for nonborder squares (with four surrounding squares) in extreme cases with $n_i \gg r_i$ and $n_j \ll r_j$, virtually all animals in a

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Fig. 3. Results of a model of sperm whale density-dependent habitat selection with shore-based whaling showing (*a*) population size (solid line for the entire study area; dottted line for the area east of 95°W) against time and CPUE against (*b*) time, (*c*) population size, and (*d*) cumulative catch.
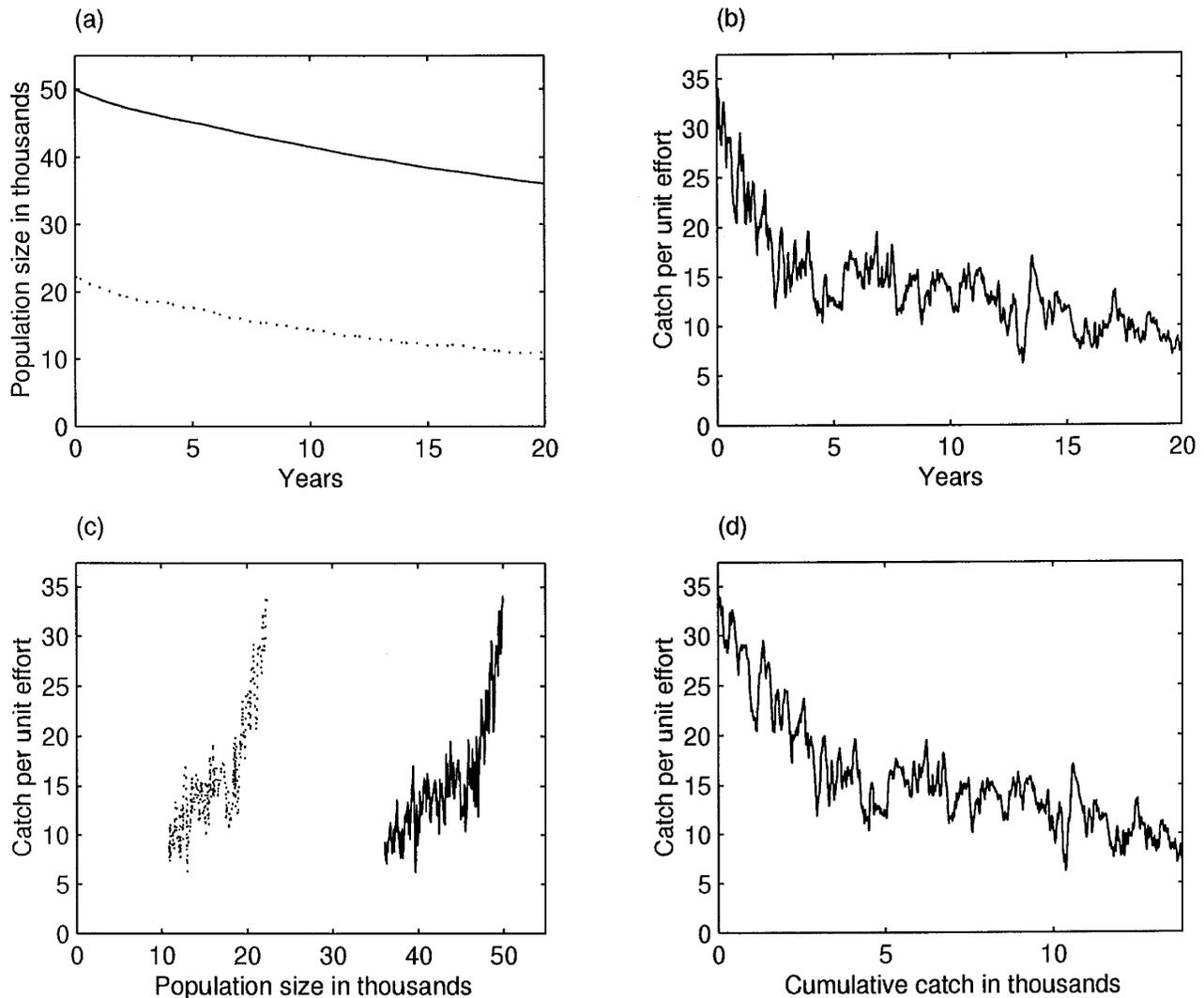
square will leave during 1 week. Parameter *b* was set to the mean resource availability over the study area (105.9 = 50 000/472). In the case of temporally variable resource availabilities, the mean migration rate out of 2° squares was about 0.12/week, translating into root mean square displacements of about 130 km/week, roughly that calculated from photographic individual identification records of female and immature sperm whales in the eastern tropical Pacific using likelihood methods (H. Whitehead, in preparation).

Four types of whaling were simulated, each assuming a constant level of effort in each week and that, in all squares being whaled, the number of whales removed during any time unit was a constant proportion of the number present at the start of a time unit (i.e., s_i is constant over whaled squares). Effort levels were such that at the end of the 19-year simulation, approximately 40% of the animals remained in the eastern part of the study area (roughly the rate of depletion achieved by nineteenth century whalers in the area; Hope and Whitehead 1991). The types of whaling were as follows.

(1) Shore-based whaling. Whaling takes place within the area bounded by 4–10°S, 78–84°W simulating the whaling from Paita, Peru, during the 1960s and 1970s (Ramirez 1989). Two percent of the whales within this area are killed each week, indicating constant effort (s_i = 0.02 in whaled squares; s_i = 0.0 elsewhere).

(2) Pelagic, open-boat whaling. Whaling takes place throughout the study area with 0.1% of the whales in each square being removed each week. This simulates the operation of a fairly large number of whaling vessels that distribute themselves proportional to whale abundance and may roughly approximate whaling by open-boat whalers working from sailing vessels during the late eighteenth and early nineteenth centuries (Whitehead and Hope 1991) (s_i = 0.001 in all squares).

(3) Pelagic, factory-fleet whaling, with scouting. Each week, whaling takes place within the one square that has the highest whale abundance. Ten percent of the whales in this square are removed during the week (s_i = 0.1 in whaled square; s_i = 0.0 elsewhere).

(4) Pelagic, factory-fleet whaling exploiting sequential sectors. This is similar to type 3, except that during each 4-year period, whaling takes place exclusively in a longitudinal swath 12° wide. The first swath is at the western end of the study area, and, as time progresses, whaling effort moves steadily from west to east. This mimics the progress of pelagic sperm whaling in the North Pacific between 1954 and 1976 (Ohsumi 1980).

Output

For each simulation, the program outputs trajectories of the total

Fig. 4. Results of a model of sperm whale density-dependent habitat selection with pelagic, open-boat whaling showing (*a*) population size (solid line for the entire study area; dotted line for the area east of 95°W) against time and CPUE against (*b*) time, (*c*) population size, and (*d*) cumulative catch.
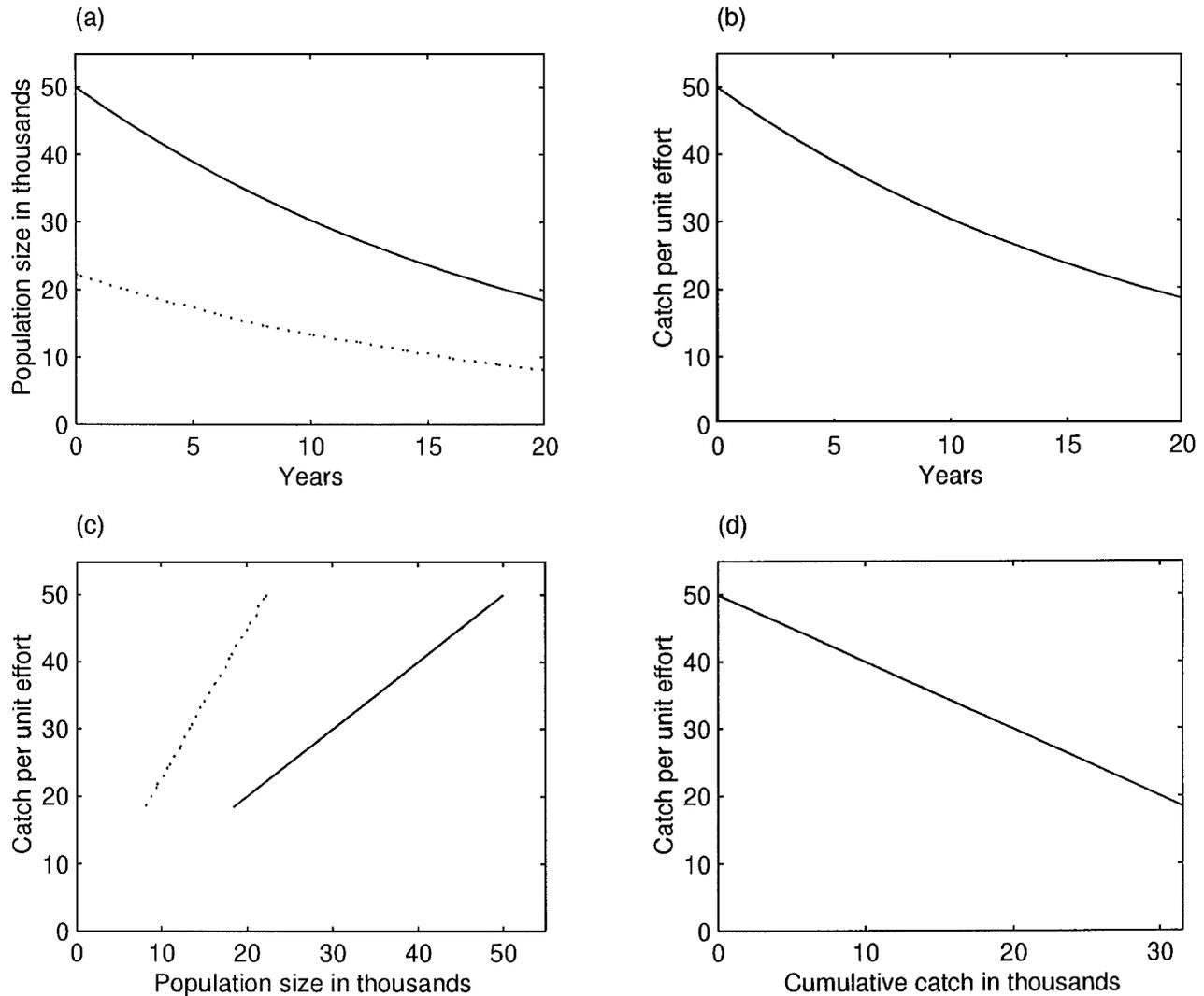
population size, as well as the population size east of 95°W, with time and trajectories of CPUE, which is proportional to catch (as effort is constant over time in all simulations). It also plots CPUE versus total population size, as well as population size east of 95°W, and CPUE versus cumulative catch. The initial population size is estimated from the *x*-intercept of a linear regression of CPUE on cumulative catch (Leslie and Davis 1939) during both the first decade of whaling and the second (to remove special conditions consequent to the initiation of exploitation).

Results

Results are shown in Table 1 and Figs. 3–6. The plots relating catch, population size, and time differed little whether resource availability was constant or variable, although there was greater variability about the trend lines with temporally variable resources. There were also no qualitative differences between replicate runs of the model with temporally variable resources. Thus, only the trajectories for the initial run with variable resource availability are shown in Figs. 3–6.

With shore-based whaling, CPUE starts high, falls quickly as the animals in the whaling area are removed, and then

levels out as the whalers catch immigrants from surrounding areas (Fig. 3), showing the "hyperdepletion" pattern of Hilborn and Walters (1992). In this situation, the CPUE trajectory bears little resemblance to changes in population size in the whole study area, the area east of 95°W, the whaling area, or any other area, however defined. The estimate of initial population size from CPUE against cumulative catch regression (Table 1) has little use, as its value depends on what time period is chosen for the regression, and it is not clear for what area the population is being estimated.

With pelagic, open-boat whaling, the situation is very different, with linear relationships between CPUE and population size of the whole area and its eastern portion (Fig. 4), as well as an accurate estimate of initial population size (Table 1).

With pelagic, factory-fleet whaling efficiently exploiting the entire study area, CPUE is monotonically related to population size (Fig. 5), although initial population size is underestimated (Table 1) because CPUE falls faster than population size.

Finally, when the study area is exploited sequentially, CPUE shows no consistent trend with time or population

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Fig. 5. Results of a model of sperm whale density-dependent habitat selection with pelagic, factory-fleet whaling showing (*a*) population size (solid line for the entire study area; dotted line for the area east of 95°W) against time and CPUE against (*b*) time, (*c*) population size, and (*d*) cumulative catch.
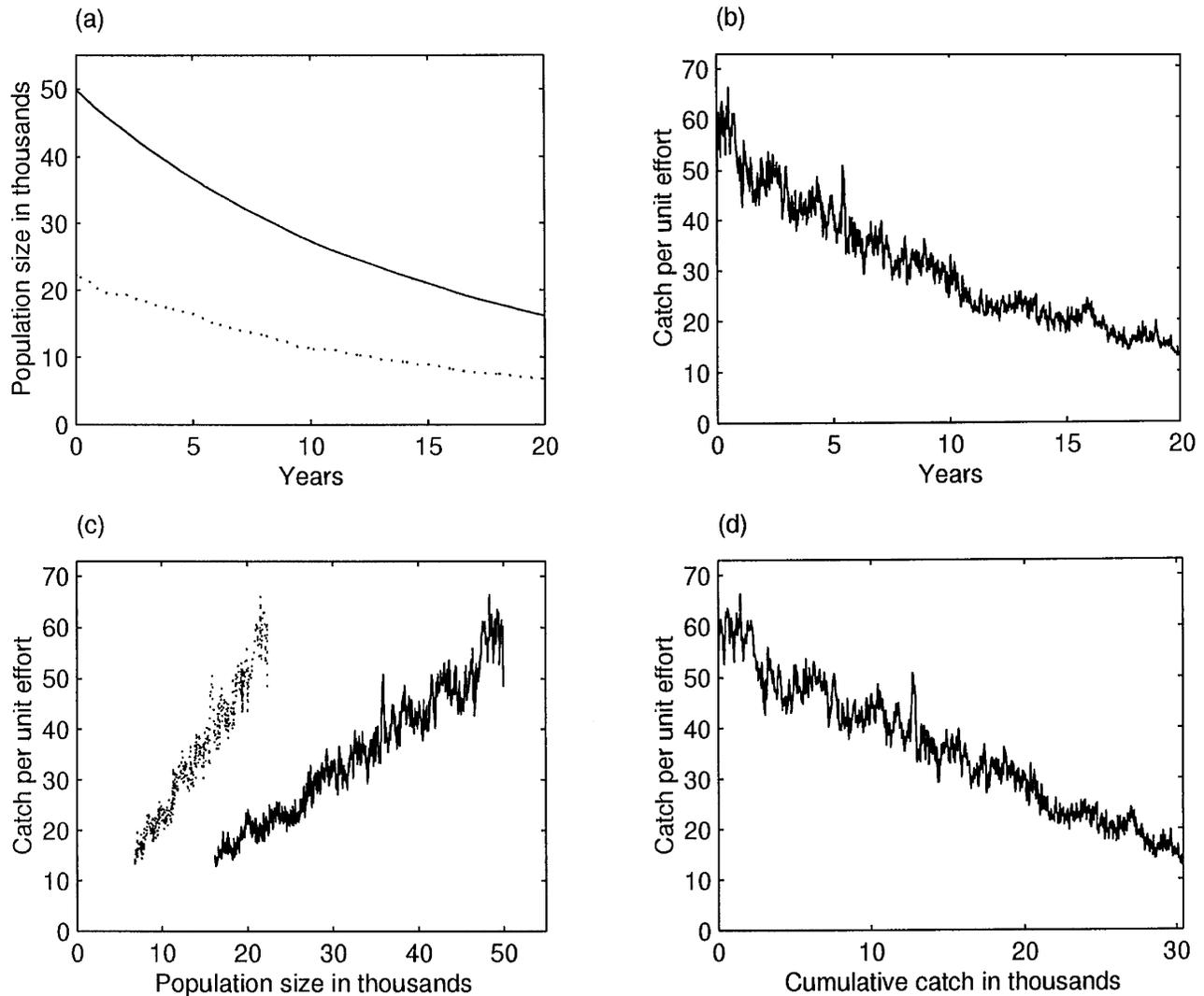
size (Fig. 6), an extreme version of the "hyperstability" pattern of Hilborn and Walters (1992). Estimates of initial population size are very variable, even between replicate runs, and sometimes negative (Table 1), indicating their lack of validity. There are quite different trends in abundance in the eastern and western parts of the study area (Fig. 6).

Discussion

### Assessing the status of sperm whale populations

This model, like all others, simplifies reality. It could be made more realistic by adding additional details of the biology of the sperm whales and the actions of the whalers (see Hilborn and Walters (1987) for possible methods and examples). Certain attributes of the animals that have been omitted from the model, such as natural mortality and recruitment, are unlikely to have much impact on the results: sperm whales have very low fecundity and natural mortality (Rice 1989) and these will effectively cancel each other out over the period of the simulation. In contrast, some assump-

tions of the model, particularly those that relate to movements, critically affect the quantitative outputs of the simulations (as expressed in Table 1 and Figs. 3–6). However (as indicated by some experimentation with input parameters), the general qualitative patterns seem quite robust. In particular, it seems reasonable to draw general conclusions about the likely validity of methods of assessing population depletion during different exploitation regimes.

CPUE

The simulations used in this paper indicate that when effort is concentrated in one part of an ocean to which whales can move from other parts, as in shore-based whaling, or when the focus of effort shifts steadily through an ocean, then CPUE has little use as a measure of the relative depletion of sperm whale stocks. In contrast, the simulations suggest that when pelagic whaling effort is reasonably uniform throughout a large and fairly isolated study area, then CPUE may be a good indicator of depletion. However, this depends on CPUE being linearly related to population density over

Fig. 6. Results of a model of sperm whale density-dependent habitat selection with pelagic, factory-fleet whaling exploiting sequential areas showing (*a*) population size (solid line for the entire study area; dotted line for the area east of 95°W) against time and CPUE against (*b*) time, (*c*) population size, and (*d*) cumulative catch.
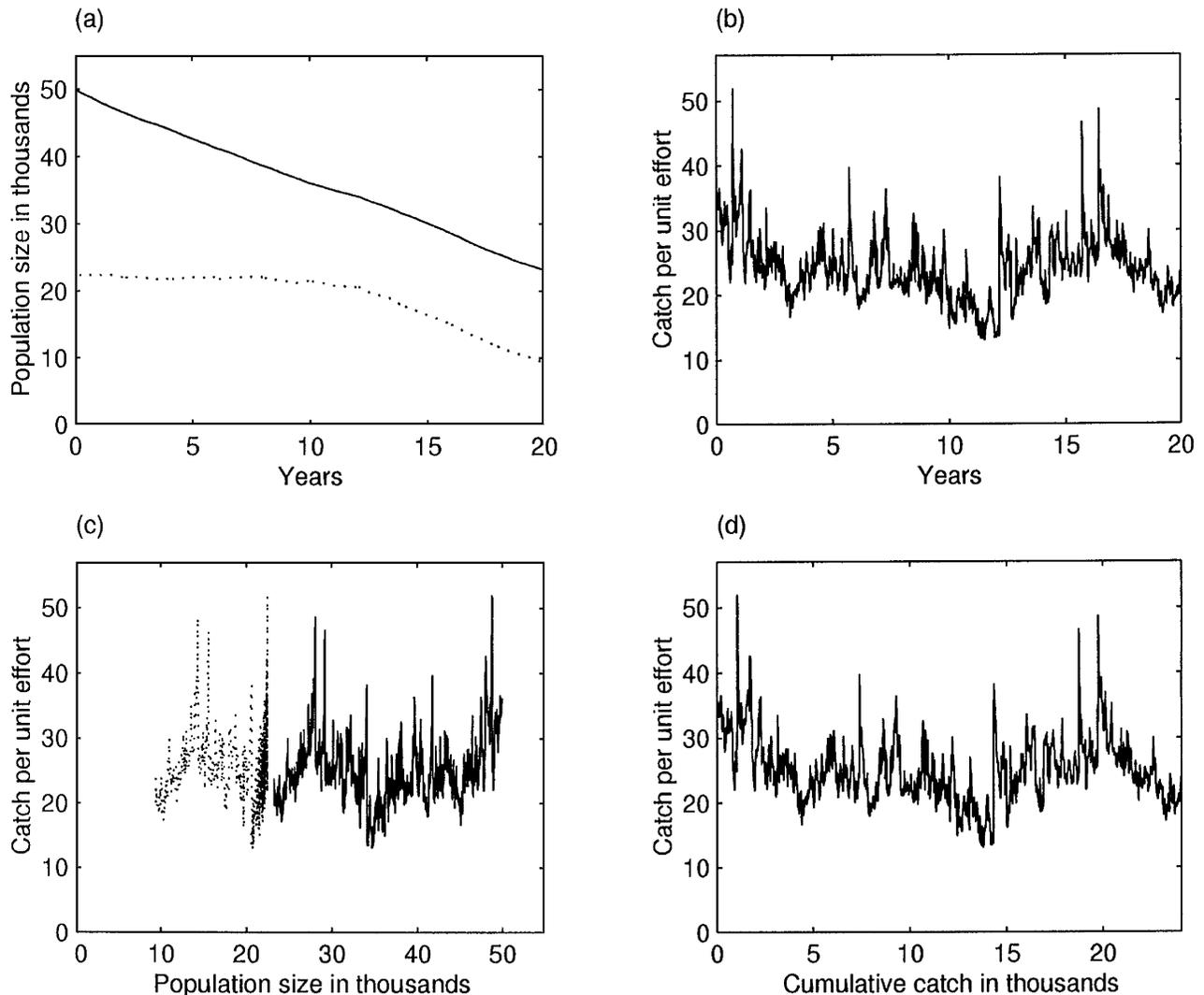
small scales. Cooke (1985) and others have examined this assumption for sperm whales, concluding that it is unlikely to be generally tenable. Thus, even without the questions of spatial dynamics considered in this paper, CPUE is usually not a good measure of sperm whale abundance.

Sightings surveys

Although this modeling does not specifically consider visual or acoustic surveys as techniques for assessing abundance, it is possible to draw some conclusions about their possible efficacy in assessing population status. If we assume that the estimated density of animals from such a survey is proportional to the population size in the survey area during the survey, then very large scale surveys can indicate the status of depletion of the population in an ocean basin. However, surveys of smaller areas may be very misleading. Estimates of density from surveys in the area of whaling operations should be approximately proportional to CPUE. However, as shown in Figs. 3 and 6, this can be very poorly related to the status of the population. In particular, with

shore-based whaling or sequential exploitation, regular surveys must extend well beyond the area in which catches are being made and sample distant regions thoroughly, if the true impact of the exploitation is to be assessed.

Even when surveys are intense, wide-ranging, and regular, the possibility of spatial or temporal variability in the relationship between the number of animals present and the density estimated from surveys can cause problems. This could result from variability in the probability of contact in different oceanographic or climatic conditions (e.g., visibility for visual surveys or background noise for acoustic surveys) or changes in whale behaviour (such as the proportion of time spent at the surface or the mean group size) with geographical area, time period, or intensity of exploitation (Cooke 1986; Whitehead 1999).

Length-specific methods

The most recent attempts to examine the effects of whaling on sperm whale populations used temporal changes in length distributions as indicators of depletion (Cooke and de

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la Mare 1983). Although I have not attempted to model length distributions, it is clear that, in the case of density-dependent habitat selection, the length distribution of catches will depend on the geographical extent of whaling and the rates of migration into the whaling area. Thus, without an accurate model of migrations, length-specific methods cannot be expected to give accurate depictions of how geographically restricted whaling operations affect sperm whale populations. Length-specific methods have other problems, summarized by Cooke (1986).

Conclusions

This consideration of density-dependent habitat selection of sperm whales adds further weight to arguments that CPUE data are not useful in assessing depletion levels of this species, except possibly in the case of very widespread geographically unrestricted pelagic whaling, as happened with eighteenth and nineteenth century open-boat whalers. It also shows that if sightings surveys are used to monitor the effects of geographically restricted whaling, then they should be carried out over a much wider area than the exploitation. If we are to monitor the effects of exploitation, or other anthropogenic threats, on sperm whale populations with any reliability, then we need a realistic model of sperm whale movement patterns.

Acknowledgements

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