Short Notes

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AN INDEX OF PER CAPITA RECRUITMENT

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Abstract

An index of per capita recruitment (*PCR*) is proposed such that

$$PCR_{y-1} = \frac{R1_y}{\left(1 - R1_y\right)e^M}$$

where $R1$ is the proportion of age-1 animals sampled in year y and M is the post-recruit mortality rate. The intent of the index is to facilitate investigation of reproductive success and the factors postulated to affect it. The formulation of *PCR* is based on the assumptions that: (i) post-recruit mortality does not vary over age or between years; (ii) 100% of age-1 animals spawn; (iii) a representative sample of the population is available; and (iv) the proportion of age-1 animals in the sample can be determined unambiguously. Normal, lognormal and uniform probability distributions of $R1$, and three levels of M were assumed in order to investigate the resulting distributions of *PCR*. Distributions of *PCR* are skewed toward higher values such that the dynamic range of *PCR* is largest with high values of $R1$; increasing M tends to offset this effect but only slightly. A simple population model was then constructed to test the sensitivity of *PCR* to relaxation of its underlying assumptions. *PCR* is not biased relative to recruits per spawner when mortality is constant over all ages and years, and when all age-1 animals spawn. These conclusions are insensitive to changes in the shape of the functional relationship between spawners and recruits. *PCR* is biased low with age-specific decline in mortality and reduction in the proportion of age-1 spawners. Introducing year-to-year random variability in both mortality and proportion of age-1 spawners resulted in broader distributions of *PCR* relative to recruits per spawner but did not appear to introduce additional bias. On average, *PCR* will underestimate recruits per spawner by 30% if reasonable assumptions are made regarding the variability of mortality and the proportion of age-1 spawners. The effectiveness of *PCR* to track changes in recruits per spawner over time was confirmed by introducing cycles in the shape of the functional relationship between spawners and recruits. *PCR* was also able to track cycles in recruits per spawner after a 20% random sampling error was added to the value of $R1$ used in the calculation of *PCR* and year-to-year random variability in mortality and proportion of age-1 spawners was introduced, although errors were larger. A time series of *PCR* for Antarctic krill (*Euphausia superba*) sampled in the vicinity of the South Shetland Islands from 1979 to 1998 is presented.

Résumé

Un indice de recrutement par tête (*PCR*) est proposé tel que

$$PCR_{y-1} = \frac{R1_y}{\left(1 - R1_y\right)e^M}$$

dans lequel $R1$ est la proportion d'individus d'âge 1 échantillonnés en l'année y et M est le taux de mortalité des post-recrues. L'objectif de l'indice est de faciliter l'étude du succès reproductif et des facteurs présumés l'affecter. La formulation de *PCR* repose sur plusieurs hypothèses : i) la mortalité des post-recrues ne varie pas en fonction de l'âge ni d'une année à une autre; ii) 100% des individus d'âge 1 se reproduisent; iii) on dispose d'un échantillon représentatif de la population; et iv) la proportion des individus d'âge 1 dans l'échantillon peut être déterminée sans ambiguïté. Les distributions de probabilité normale, lognormale et uniforme de $R1$, ainsi que trois niveaux de M sont avancés afin d'étudier les distributions obtenues de *PCR*. Ces dernières distributions sont biaisées à la

hausse pour que l'intervalle dynamique le plus élevé de *PCR* corresponde aux valeurs élevées de *R*1; toute augmentation de la valeur de M tend à contrebalancer très légèrement cet effet. Un modèle simple de la population est ensuite élaboré pour tester la sensibilité de *PCR* à un assouplissement des hypothèses fondamentales. Le *PCR* n'est pas biaisé relativement aux recrues par reproducteur lorsque la mortalité est constante pour tous les âges et toutes les années, et lorsque tous les individus d'âge 1 se reproduisent. Ces conclusions ne sont pas sensibles aux changements dans la forme de la relation fonctionnelle entre les reproducteurs et les recrues. Le *PCR* est biaisé à la baisse avec le déclin spécifique à l'âge de la mortalité et la réduction de la proportion des reproducteurs d'âge 1. L'introduction d'une variabilité aléatoire d'année en année tant de la mortalité que de la proportion des reproducteurs d'âge 1 a pour résultat des distributions plus larges de *PCR* relativement aux recrues par reproducteur mais ne semble pas introduire de biais supplémentaire. En moyenne, le *PCR* sous-estimera les recrues par reproducteur de 30% si les hypothèses avancées sont raisonnables en ce qui concerne la variabilité de la mortalité et la proportion des reproducteurs d'âge 1. L'efficacité du *PCR* pour suivre les changements de recrues par reproducteur au fil du temps est confirmée par l'introduction de cycles sous la forme de relation fonctionnelle entre les reproducteurs et les recrues. Le *PCR* est également capable de suivre les cycles de recrues par reproducteur, une fois une erreur aléatoire d'échantillonnage de 20% ajoutée à la valeur de *R*1 utilisée dans le calcul du *PCR* et qu'une variabilité aléatoire d'année en année de la mortalité et de la proportion des reproducteurs d'âge 1 a été introduite, bien que les erreurs soient plus importantes. Une série chronologique de *PCR* est présentée pour le krill antarctique (*Euphausia superba*) échantillonné à proximité des îles Shetland du Sud de 1979 à 1998.

Резюме

В статье предложен следующий показатель пополнения на особь криля (*PCR*):

$$PCR_{y-1} = \frac{R1_y}{\left(1 - R1_y\right)e^M}$$

где $R1$ – доля 1-летних особей в выборке в год y, а M – смертность после вступления в пополнение. Показатель предназначен для исследования репродуктивного успеха и влияющих на него факторов. Формулировка *PCR* основана на допущениях, что: (i) смертность после вступления в пополнение не меняется по возрасту или по годам; (ii) нерестится 100% 1-летних особей; (iii) имеется репрезентативная выборка популяции; и (iv) в выборке можно однозначно определить долю 1-летних особей. Для анализа распределения *PCR* были приняты нормальное, логнормальное и равномерное распределения вероятностей $R1$ и 3 значения M. Распределения *PCR* сдвинуты в сторону более высоких значений, так что наибольший динамический диапазон *PCR* достигается с высокими значениями $R1$; увеличение M имеет незначительный обратный эффект. Для проверки чувствительности *PCR* к ослаблению допущений была создана простая модель популяции. *PCR* не смещен по сравнению с числом рекрутов на нерестящуюся особь, если смертность постоянна по возрастам и годам, и нерестятся все 1-летние особи. Эти результаты не зависят от изменений формы функциональной зависимости между нерестящимися особями и рекрутами. *PCR* сдвинут вниз при повозрастном сокращении смертности и уменьшении доли 1-летних нерестящихся особей. Введение в показатель смертности и долю 1-летних нерестящихся особей погодовой случайной изменчивости привело к более широким распределениям *PCR* по сравнению с числом рекрутов на нерестящуюся особь, но не внесло заметного дополнительного сдвига. В среднем при разумных допущениях в отношении изменчивости смертности и доли 1-летних нерестящихся особей *PCR* дает заниженную (на 30%) оценку числа рекрутов на нерестящуюся особь. Введение цикличности в форму функциональной зависимости между нерестящимися особями и рекрутами подтвердило эффективность *PCR* для прослеживания изменений в числе рекрутов на нерестящуюся особь по времени. *PCR* также позволял прослеживать цикличные изменения в пополнении на нерестящуюся особь после добавления к использовавшемуся для расчета значению $R1$ 20%-ной ошибки случайного отбора и введения погодовой случайной изменчивости в

показатель смертности и долю 1-летних нерестящихся особей, хотя ошибки были больше. Представлены временные ряды *PCR* за 1979–1998 гг. для Антарктического криля (*Euphausia superba*), выловленного в районе Южных Шетландских о-вов.

Resumen

Se propone un índice de reclutamiento per cápita (*PCR*) tal que

$$PCR_{y-1} = \frac{R1_y}{\left(1 - R1_y\right)e^M}$$

donde $R1$ es la proporción de animales de 1 año de edad muestreados en un año y, y M es la tasa de mortalidad después del reclutamiento. El objetivo del índice es facilitar la investigación del éxito reproductor y de los factores que supuestamente le afectan. La formulación del *PCR* se basa en las siguientes suposiciones: (i) la mortalidad posterior de reclutas no cambia con la edad o de un año a otro; (ii) 100% de los animales de un año desovan; (iii) se dispone de una muestra representativa de la población; y (iv) la proporción de animales de 1 año en la muestra puede determinarse sin ambigüedad. Se adoptaron distribuciones normales, lognormales y uniformes de la probabilidad de $R1$, y tres niveles de M a fin de investigar las distribuciones resultantes de *PCR*. Las distribuciones de *PCR* están sesgadas hacia valores más altos de manera que el margen dinámico de *PCR* es mayor cuando los valores de $R1$ son altos; un aumento en M tiende a compensar levemente este efecto. Se elaboró un modelo simple de la población para estudiar la sensitividad de *PCR* a una relajación de las suposiciones básicas. El *PCR* no está sesgado en relación a los reclutas por reproductor cuando la mortalidad se mantiene constante a través de los años y edades, y cuando todos los animales de 1 año desovan. Estas conclusiones no son afectadas por los cambios en la forma de la relación funcional entre reproductores y reclutas. El sesgo del *PCR* tiende a la subestimación debido a la disminución de la mortalidad relacionada específicamente con la edad y la reducción en la proporción de reproductores de 1 año de edad. La introducción de variabilidad al azar de un año a otro en la mortalidad y en la proporción de reproductores de 1 año produjo distribuciones más amplias de *PCR* en relación con los reclutas por reproductor, pero no parece haber introducido un sesgo adicional. En general, el *PCR* subestimará en 30% el número de reclutas por reproductor si se hacen suposiciones razonables en cuanto a la variabilidad de la mortalidad y la proporción de reproductores de 1 año. Se confirmó la eficacia del *PCR* en la detección de cambios en los reclutas por reproductor en el tiempo mediante la introducción de ciclos de forma idéntica a la de la relación funcional entre reproductores y reclutas. El *PCR* también sirvió para detectar ciclos en los reclutas por reproductor después de introducir un error de muestreo aleatorio de 20% al valor de $R1$ utilizado en el cálculo de *PCR*, y también después de introducir una variabilidad aleatoria en la mortalidad anual y en la proporción de reproductores de 1 año, pero los errores fueron mayores. Se presenta una serie cronológica de *PCR* para el kril antártico (*Euphausia superba*) muestreado en los alrededores de las islas Georgias del Sur de 1979 a 1998.

Keywords: reproductive success, reproductive performance, year class strength, CCAMLR

INTRODUCTION

Results of field studies conducted in the South Shetland Islands suggest that the population of Antarctic krill (*Euphausia superba*) in the southwest Atlantic sector of the Southern Ocean is sustained by occasional strong year classes, that adult reproductive output and pre-recruit survival are affected by physical and biological factors, and that monitoring these factors will allow short-term prediction of population growth (Siegel and Loeb, 1995; Loeb et al., 1997). These hypotheses are supported by evidence for multi-year coherence among physical and biological parameters throughout the southwest Atlantic sector (Report of the Workshop on Area 48, see SC-CAMLR, 1998).

These studies employed estimates of proportional recruitment ($R1$) as an index of the reproductive performance of krill when testing correlations between reproductive performance and factors

postulated to affect it. Estimates of *R*1 are derived from an analysis of krill length-density data from net samples (de la Mare, 1994) where *R*1 is defined as the proportion of individuals in a given year of sampling that fall within the year-1 age class. *R*1 is indexed to the preceding year, the year in which age-1 krill were spawned*.

As a measure of reproductive performance *R*1 combines two processes which may or may not be independent: (i) the intensity, timing and duration of spawning; and (ii) the survival of young through the egg and larval stages. While it may be appropriate to monitor these processes separately, no time series of observations of Antarctic krill are available to do so. Alternatively, krill length-density distributions are available from annual surveys in the South Shetland Islands conducted over the last two decades. Strong year classes are evident in this time series, first appearing as a large mode at 20 to 30 mm length and in subsequent years as progressively longer length modes (Figure 1). The 20-year time series of *R*1 constructed from these observations (Siegel et al., 1998) has been used in studies that attempt to identify the factors that control krill reproductive performance.

In addition to compounding the results of two processes, the use of *R*1 presents some interpretive problems. Because *R*1 is a proportion, bounded by 0 and 1, relative measures of reproductive performance between years may be distorted, particularly at the high and low extremes. A more appropriate measure would be the number of recruits per spawner, or per capita recruitment (*PCR*). Such a measure could be obtained with surveys in successive years provided that each survey circumscribed the same portion of the population range. Unfortunately, this is rarely the case. For the South Shetlands' surveys, the survey area was fixed but the proportion of the population within the area may have varied from year to year.

As an interim solution, this note presents a possible index of *PCR* that is derived from an estimate of *R*1 and several assumptions regarding natural mortality. The index is a proxy for the number of recruits per spawner, where recruits and spawners are estimated from the same sample. Recruits are estimated as the number of age-1 animals in the population and spawners are estimated as the number of older animals adjusted for one year of mortality. Similar to *R*1, the index would measure the effectiveness of both spawning and survival of pre-recruits. The intent of the index is to facilitate investigation of reproductive success and the factors postulated to affect it.

In the following sections the index is derived and its statistical properties relative to those of *R*1 are described. The behaviour of the index is investigated when the assumptions regarding natural mortality are relaxed, and where recruitment is specified (i) as a fixed function of spawners and (ii) as a cyclic function of spawners. In the final section, the time series of *R*1, derived from length-density distributions in the South Shetland Islands, is converted to a series of *PCR* indices for Antarctic krill.

DERIVATION OF AN INDEX OF *PCR*

The *PCR* index can be defined as the ratio of the number of age-1 animals and the number of spawners that produced them. This may be approximated as the ratio of age-1 animals to the rest of the recruited population with one year of mortality removed:

$$PCR_{y-1} = \frac{(NR1)_y}{(NR2)_y e^{(M_2)_{y-1}} + (NR3)_y e^{(M_3)_{y-1}} + (NR4)_y e^{(M_4)_{y-1}} + \ldots}$$

where N is the population size; $R1$, $R2$, $R3$, $R4$ ... are the proportions of N that are in the age-1, age-2, age-3, age-4 ... year classes; M_2, M_3, M_4 ... the post-recruit mortality rates for age-2, age-3, age-4 ... year classes; and y is an index of year. If it is assumed that post-recruit mortality is constant over all classes, the above expression reduces to:

$$PCR_{y-1} = \frac{R1_y}{(1 - R1_y)e^{M_{y-1}}}.$$

This formulation can be extended over a series of years by assuming that the variability of post-recruit mortality is negligible when compared to the variability of reproductive output and pre-recruit survival:

$$PCR_{y-1} = \frac{R1_y}{(1 - R1_y)e^{M}}.$$

* Proportional recruitment should not be confused with absolute recruitment or the number of age-1 animals entering the adult population. It is possible that a high value of *R*1 during a period of low abundance is associated with lower absolute recruitment than a low value of *R*1 during a period of high abundance.

An estimate of *PCR* can be generated from a sample of the population if it is assumed that a representative sample is available in the form of a length-density distribution and that the proportion of age-1 animals ($R1$) can be unambiguously determined. With respect to generating a time series of *PCR*, it is not necessary to assume that the same proportion of the population is sampled each year, only that the sample is representative of the total population.

Implicit in the above formulation is the assumption that animals are fully recruited to the adult population (i.e. spawn) at age-1. As such, *PCR* can be calculated from the estimate of a single population parameter ($R1$) and an assumed mortality rate. Antarctic krill, however, appear to spend one to two years in the juvenile and sub-adult stages and may not spawn until age 2 or age 3 (Siegel, 1987). Because the denominator includes non-spawners, *PCR* will therefore tend to underestimate the true recruits per spawner. Alternatively, the *PCR* index could be reformulated to account for non-spawners. This would require at least three additional parameters: the proportion of age-1 animals that are not spawning, the proportion of age-2 animals in the population and the proportion of age-2 animals that are not spawning. In this paper I have used the simpler formulation, with the understanding that the index will be negatively biased to the extent that krill delay reproduction. The extent of this bias with respect to spawning by age-1 animals is explored in subsequent sections.

STATISTICAL PROPERTIES

As proposed, the *PCR* index is based on a transformation of $R1$ and an assumption of M. Unlike $R1$, which is constrained between zero and one, *PCR* can range from zero to infinity, as $R1$ approaches 1.

The statistical properties of *PCR* may be examined by plotting the distribution of *PCR* under various assumptions regarding the frequency distribution of $R1$ and the assumed value of M. Three distributions, each with a mean of 0.5, were assumed for $R1$: (i) normal with a standard deviation of 0.1; (ii) lognormal with a standard deviation of 0.5; and (iii) uniform. $R1$ was further constrained to $0 \leq R1 < 1$. M ranged between 0.6 and 1.0*. For each frequency distribution of $R1$, 1 000 values were drawn at random and *PCR* calculated for several levels of M.

When $R1$ followed a normal distribution with a mean of 0.5 and a standard deviation of 0.1, the distribution of *PCR* was skewed slightly toward higher values (skewness = 2.4). When the level of mortality increased, the mean and mode of the distributions of *PCR* decreased, although the rate of change was slower with increasing mortality. Skewness of the distributions of *PCR* remained constant with changes in the level of mortality.

When $R1$ followed a lognormal distribution with a mean of 0.5 and a standard deviation of 0.5, the distribution of *PCR* was more skewed toward higher values (skewness = 23.0). As expected, increasing levels of mortality caused the mean and mode of the distribution of *PCR* to decrease, although the rate of change slowed with increasing mortality.

When $R1$ followed a uniform distribution with a mean of 0.5, the distribution of *PCR* was highly skewed toward higher values (skewness = 28.4). Again, increasing levels of mortality caused the mean and mode of the distribution of *PCR* to decrease, although the rate of change slowed with increasing mortality.

The dynamic range of *PCR* thus increases with an increase in $R1$, but decreases with an increase in M (Figure 2). This is an advantage if small changes in $R1$ are to be detected, particularly at the higher values, which will tend to drive population growth. Small changes in the assumed value of M, particularly at high levels, will not greatly affect the value of *PCR* over the normal range of $R1$. The effect will become greater, however, at very high values of $R1$.

RELAXATION OF ASSUMPTIONS

FIXED RECRUITMENT

In order to investigate the sensitivity of *PCR* to the various assumptions, a simple population time series was modelled. In this exercise, recruitment was determined and the other parameters were varied.

* Siegel (1992) estimated the natural mortality (M) of krill was between 0.88 and 0.96 from catch-at-age data. Priddle et al. (1988) estimated M to range between 0.8 and 1.35 based on estimates of the von Bertalanffy growth constant (K) and an assumed relationship between M and K. Siegel and Kalinowski (1994) estimated M to range between 0.66 and 0.92 based on an assumed relationship between longevity and mortality (Alagaraja, 1984).

Seven age classes constituted the recruited population and the number of spawners equalled the total of all age classes. Mortality was fixed across all ages or set to decline exponentially, such that:

$$M_i = M_1 e^{-a(i-1)}$$

where $i > 1$ indexes age class and a was the rate at which mortality declined exponentially with age. When $a = 0$, mortality was constant over all ages; as a increased, age-specific mortality decreased at a more rapid rate.

A Beverton and Holt formulation was used to define the numbers of recruits (R) as a function of spawners (S), such that:

$$R = \frac{R_{max} S}{b + S}$$

where R_{max} was the maximum number of recruits and b was the number of spawners that produced 0.5 R_{max}. When b was small relative to S there was little dependence of R on S and maximum recruitment was possible over a wide range of spawners. As b increased relative to S there was more dependence of R on S.

The proportion of age-1 spawners (c) varied from 0 to 1, such that:

$$S = cN_1 + N_2 + N_3 + N_4 + \ldots .$$

If $c = 1$ all age-1 animals spawned; as c approaches zero fewer age-1 animals spawned. Note that this assumes that all age-2 animals spawn, which may not be the case (Siegel, 1987). Partial spawning by age-2 animals could have been accommodated by adding another parameter. Similar to c, the effect of this parameter would have been to reduce the number of spawners, albeit to a lesser degree because N_2 is reduced relative to N_1 by mortality.

The model was seeded with 1 000 age-1 animals and R_{max} set to the same value. The number of spawners divided into the number of age-1 recruits the following year (R/S) was defined as the real PCR and compared to PCR calculated from $R1$. The model was reiterated with a fixed set of parameters until convergence was achieved and the population was at equilibrium (usually less than 50 iterations). As an example, if $M_1 = 0.8$, $a = 0$ (M constant over all ages), $b = 100$ (recruitment relatively independent of spawners), and $c = 1$ (all age-1 animals spawn), the following results:

Age 1 (R)	Age 2	Age 3	Age 4	Age 5	Age 6
944.73	424.49	190.74	85.70	38.51	17.30

Age 7	Spawners (S)	R/S	$R1$	PCR	$\frac{PCR}{R/S}$
7.77	1 709.25	0.553	0.553	0.555	1.005

Although the size of the equilibrium spawning population responds to changes in b, the equilibrium values of R/S and PCR do not. For $b = 1\ 000$ and $c = 1$ the following results:

Age 1 (R)	Age 2	Age 3	Age 4	Age 5	Age 6
447.29	200.98	90.31	40.58	18.23	8.19

Age 7	Spawners (S)	R/S	$R1$	PCR	$\frac{PCR}{R/S}$
3.68	809.25	0.553	0.553	0.555	1.005

The small difference between R/S and PCR (positive bias) results from the contribution of the oldest age class, which has left the population by the following year and is not accounted for in the calculation of PCR. This effect is diminished with higher values of M and larger with lower values of M, which controls the number of animals in the oldest age class. Similarly, increasing the rate at which mortality declines with age (a) has the effect of increasing the proportion of animals in the oldest age class, while causing an underestimate of the true M used in the calculation of PCR. This results in the largest negative bias between R/S and PCR at high values of M_1 and a. If $M_1 = 1.0$, $a = 0.5$, $b = 100$ and $c = 1$, the following results:

Age 1 (R)	Age 2	Age 3	Age 4	Age 5	Age 6
966.24	526.83	364.67	291.74	254.82	234.73

Age 7	Spawners (S)	R/S	$R1$	PCR	$\frac{PCR}{R/S}$
223.33	2 862.38	0.338	0.338	0.187	0.555

The effects of M_1 and a on the ratio of PCR and R/S are described in Figure 3 where it can be seen that a has the largest effect.

The bias between PCR and R/S increases more if less than 100% of age-1 animals spawn. If $M_1 = 0.8$, $a = 0.0$, $b = 100$ and $c = 0$ the following results:

Age 1 (R)	Age 2	Age 3	Age 4	Age 5	Age 6
876.43	393.80	176.95	79.51	35.73	16.05

Age 7	Spawners (S)	R/S	$R1$	PCR	$\frac{PCR}{R/S}$
7.21	709.25	1.236	0.553	0.555	0.449

The ratio of PCR and R/S is further reduced to 0.325 if half of age-2 animals spawn and to 0.200 if no age-2 animals spawn.

As a worse-case scenario, if $M_1 = 1.0$, $a = 0.5$, $b = 100$ and $c = 0$ (no age-1 animals spawn) the following results:

Age 1 (R)	Age 2	Age 3	Age 4	Age 5	Age 6
949.04	517.45	358.18	286.55	250.28	230.56

Age 7	Spawners (S)	R/S	$R1$	PCR	$\frac{PCR}{R/S}$
219.36	1 862.38	0.510	0.338	0.187	0.368

The bias of PCR relative to R/S can be visualised by examining the surface of $PCR/(R/S)$ as a function of M_1 and c for three levels of a (Figure 4). Decreasing c from 1 to 0 increases the negative bias of PCR relative to R/S for all levels of a, such that when $c = 0$ the same degree of bias exists across all levels of M_1. Increasing a results in a reduction of the range of $PCR/(R/S)$ over the field of c and M_1. The largest contributor to bias between PCR and R/S is variation in c, the proportion of age-1 animals that spawn. Partial spawning by age-2 animals would further increase the bias such that the ratio of PCR to R/S would be 0.317 if half of age-2 animals spawn and to 0.266 if no age-2 animals spawn.

Year-to-year random variability in mortality was introduced by restarting the model at its equilibrium state and allowing M_1 to vary such that:

$$(M_1)_j = M_1^* + \sum_j \varepsilon$$

where $(M_1)_j$ is age-1 mortality in the jth iteration, M_1^* is the initial value of M_1 and ε is a random variable. The model was reiterated 1 000 times and the distribution of R/S compared with the distribution of PCR.

When ε followed a normal distribution with a mean of 0 and a standard deviation of 0.1, $M_1^* = 0.8$, $a = 0$, $b = 100$ and $c = 1$, the distributions of R/S and PCR were near normal in shape. The distribution of PCR was broader than that of R/S, but the distribution of $PCR/(R/S)$ had a mode near 1, suggesting that the expected bias is negligible. When ε followed a uniform distribution with a range between -0.2 and +0.2, the distribution of R/S was uniform, but the distribution of PCR was non-uniform with lower values more common than higher ones. The distribution of $PCR/(R/S)$ was also non-uniform with lower values more common than higher ones, but asymmetrical about 1 such that the mean of the distribution is near 1. In both cases, when a was allowed to increase PCR became negatively biased relative to R/S (expected value of $PCR/(R/S)$ was 0.885 and 0.634 for $a = 0.1$ and 0.5 respectively).

Year-to-year random variability in the proportion of age-1 spawners was introduced by allowing c to vary between 0 and 1 and reiterating the model 1 000 times. When c followed a uniform distribution, $M_1 = 0.8$, $a = 0$ and $b = 100$, the expected value of $PCR/(R/S)$ was 0.727. The negative bias of PCR relative to R/S increased with increasing a (expected value of $PCR/(R/S)$ was 0.665 and 0.541 for $a = 0.1$ and 0.5 respectively).

A more realistic expectation of the behaviour of PCR relative to R/S may be obtained by making some reasonable assumptions. First, let M_1 range from 0.6 to 1.0 with a uniform distribution; i.e. high age-1 mortality is equally plausible as low age-1 mortality and any value in between. Second, let $a = 0$; i.e. if high mortality is experienced by age-1 animals during a particular year the same will be true for all ages. Third, let c range from 0 to 1 with a uniform distribution, but allow it to be correlated with ε ($r^2 = -0.7$); i.e. conditions that are associated with low mortality tend to also be associated with precocious spawning and vice versa. As before, the model was reiterated 1 000 times and the distribution of R/S compared with the distribution of PCR. The distribution of R/S showed no central tendency with lower values more common than higher values. The distribution of PCR was more uniform and the distribution of $PCR/(R/S)$ was asymmetrical about a mean of 0.712. As noted above, the expected value of $PCR/(R/S)$ would be even lower if partial spawning by age-2 animals was considered.

In summary:

(i) The equilibrium values of the population model indicate negligible bias between PCR

and *R/S* when mortality does not decline with age and when all age-1 animals spawn.

(ii) Under these circumstances *PCR* slightly overestimates *R/S* because the spawning contribution of the last age class is not considered in the calculation of *PCR*.

(iii) Changing the shape of the recruit-spawner curve (modifying *b*) changes the equilibrium spawning population but has no effect on the ratio of *PCR* and *R/S*.

(iv) Increasing the rate at which mortality declines with age (increasing *a*) causes *PCR* to underestimate *R/S* and this effect increases with the value of M_1, the mortality of age-1 animals.

(v) Decreasing the proportion of age-1 animals that spawn (decreasing *c*) also results in *PCR* underestimating *R/S*.

(vi) When random variability is introduced for M_1 or *c*, the resulting distributions of *PCR* broaden relative to *R/S* but additional bias does not appear to be introduced.

(vii) When correlated random variability is introduced for M_1 and *c*, and *a* is set to 0.0, *PCR* underestimates *R/S* by an average of approximately 30%.

RELAXATION OF ASSUMPTIONS
VARIABLE RECRUITMENT

Another way to examine the performance of *PCR* as an index of change in reproductive success is to redefine recruitment as a cyclic function of spawners such that:

$$b_i = \frac{b_{max}}{2}\left(1+\sin\left(\frac{2\pi(i)}{p}\right)\right)$$

where *i* is the iteration number, and *b* cycles between 0 and b_{max} with a period of *p* iterations. As reproductive success varies over time the ability of *PCR* to track changes in *R/S* can be checked. For this exercise b_{max} was set to 1 500 and *p* was set to five iterations. If $M_1 = 0.8$, $a = 0$ and $c = 1$, *PCR* follows the cycles of *R/S* without bias (Figure 5a). The same is true for all levels of M_1 except that the range of oscillations in *R/S* and *PCR* are greater with higher levels of M_1. With increasing values of *a*, *PCR* continues to follow the cycles of *R/S* but with a negative bias that varies over a relatively small range (Figure 5b). With decreasing values of *c*, *PCR* follows the cycles of *R/S* but also with a negative bias that is largest at high values of *R/S* and smallest at low values (Figure 5c). *PCR* will still follow the cycles of *R/S* if M_1 and *c* are allowed to vary randomly but the bias between *PCR* and *R/S* is larger and not correlated with the phase of the cycle (Figure 6a).

The effects of sampling errors were examined by adding a random error term to *R*1 prior to calculating *PCR*. The error term was uniformly distributed about *R*1 with a range of ±20%. If $M_1 = 0.8$, $a = 0$ and $c = 1$, *PCR* follows the cycles of *R/S* with *PCR/(R/S)* ranging from 0.8 to 1.2 (Figure 6b). *PCR* will still follow the cycles of *R/S* if M_1 and *c* are allowed to vary randomly but *PCR/(R/S)* varies asymmetrically about 1 and not correlated with the phase of the cycle (Figure 6c).

In summary, *PCR* is able to track cycles in recruits per spawner (*R/S*) under the following conditions: (i) mortality does not decline with age ($a = 0$) and when all age-1 animals spawn ($c = 1$); (ii) ±20% random sampling error in the estimate of *R*1; (iii) random year-to-year variability in mortality (0.6 to 1.0) and *c* (0 to 1); and (iv) the inclusion of both sampling error in the estimate of *R*1 and variability in mortality and *c*. Increasing *a* and decreasing *c* causes *PCR* to underestimate *R/S*, with the bias more pronounced at high levels relative to low levels of *R/S*.

It is also clear from these simulations that *PCR* is a better index of *R/S* than *R*1. As formulated in this note, *PCR* is calculated from a single year's sample of the krill population as a simple function of *R*1 and an assumed post-recruit mortality rate. As such, it is only an incremental improvement to the use of *R*1. Other improvements may be obtained by better characterisation of post-recruit mortality, provision for non-spawning age-1 and age-2 animals, and the inclusion of samples from more than one year.

APPLICATION TO
ANTARCTIC KRILL

Assuming that *M* was equal to 0.8, a series of *R*1 values, estimated from krill length-density distributions obtained from sampling in the South Shetland Islands (Loeb et al., 1997), was used to generate a corresponding series of *PCR* values:

Year	*R1*	*PCR*
1978/79	0.069	0.033302
1979/80	0.599	0.671192
1980/81	0.757	1.399761
1981/82	0.663	0.883991
1982/83	0.119	0.060693
1983/84	0.214	0.122336
1984/85	0.175	0.095312
1985/86	0.633	0.775001
1986/87	0.291	0.184421
1987/88	0.275	0.170435
1988/89	0.063	0.030211
1989/90	0.099	0.049371
1990/91	0.587	0.638635
1991/92	0.012	0.005457
1992/93	0.029	0.013420
1993/94	0.125	0.064190
1994/95	0.622	0.739372
1995/96	0.198	0.110932
1996/97[1]	0.120	0.061272
1997/98[1,2]	0.0001	0.000045

[1] V. Loeb and V. Siegel, pers. comm.
[2] Reported as 0 but changed to 0.0001 for computational reasons.

Relatively good reproductive success is apparent from spawning during the summers of 1980/81, 1987/88, 1990/91 and 1994/95 (Figure 7). *PCR* as an index of reproductive success is higher than *R1* in all of these years except for the moderate year class of 1990/91. The non-linear transformation of *R1* to *PCR* results in *PCR* being less than *R1* at low values and higher than *R1* at high values. The crossover, where *PCR* is greater than *R1*, is at an *R1* value of approximately 0.55 (Figure 7) when it is assumed that *M* was equal to 0.8.

If actual mortality is larger than assumed or if the proportion of spawners in any year class is less than 1, then the fraction of spawners in the population will be overestimated and *PCR* will represent an underestimate of recruits per spawner. Under most conditions therefore *PCR* may be considered a conservative estimate (i.e. an underestimate) of recruits per spawner.

CONCLUSION

A simple index of reproductive success is proposed as a function of the proportion of age-1 animals in the population and the post-recruit mortality rate. The intent of the index is to facilitate investigation of reproductive success and the factors postulated to affect it. The index can be considered a proxy measurement of recruits per spawner and as such combines two process: (i) the intensity and, timing and duration of spawning; and (ii) the survival of young through the egg and larval stages. The formulation of the index is based on assumptions that: (i) post-recruit mortality does not vary over age or between years; (ii) 100% of age-1 animals spawn; (iii) a representative sample of the population is available; and (iv) the proportion of age-1 animals in the sample can be determined unambiguously. A simple age-structured model was used to demonstrate that: (i) the index was biased low if post-recruit mortality decreased with increasing age or if not all age-1 or age-2 animals spawned; (ii) random variability in mortality and/or proportion of age-1 spawners did not introduce additional bias; (iii) the index was able to track cycles in recruits per spawner even after the introduction of random variability in mortality and the proportion of age-1 spawners, and a 20% sampling error. The index may be considered a better measure of recruits per spawner than the proportion of age-1 animals in the population. Under most circumstances, however, the index may be considered a conservative estimate (i.e. an underestimate) of recruits per spawner.

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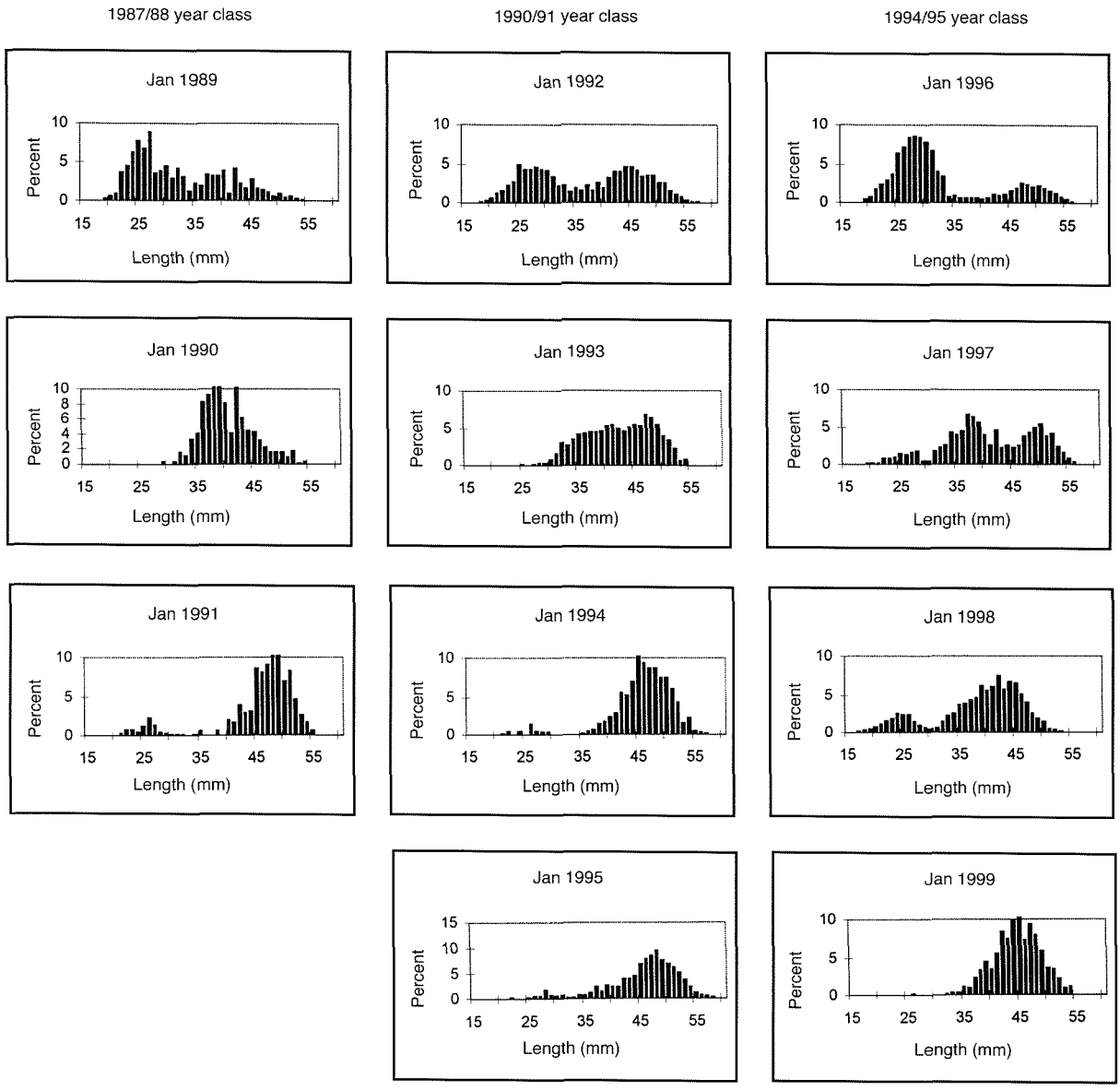


Figure 1: Krill length-density distributions sampled over the period 1990–1999. Three strong year classes (1988, 1991 and 1995) are first evident when sampled as age-1 animals. In the intervening years without strong year classes the dominant length mode is shifted progressively larger until another strong year class is produced.

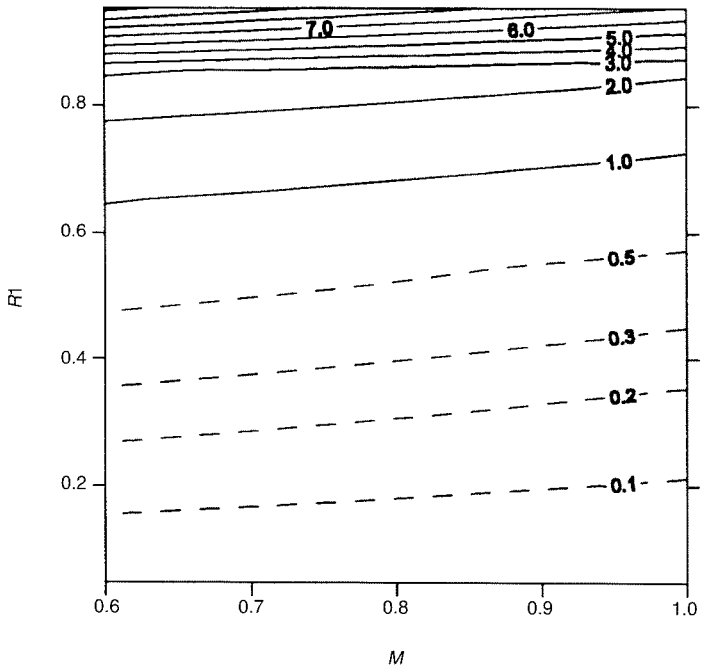


Figure 2: Surface plot of *PCR* as a function of *R*1 and *M*.

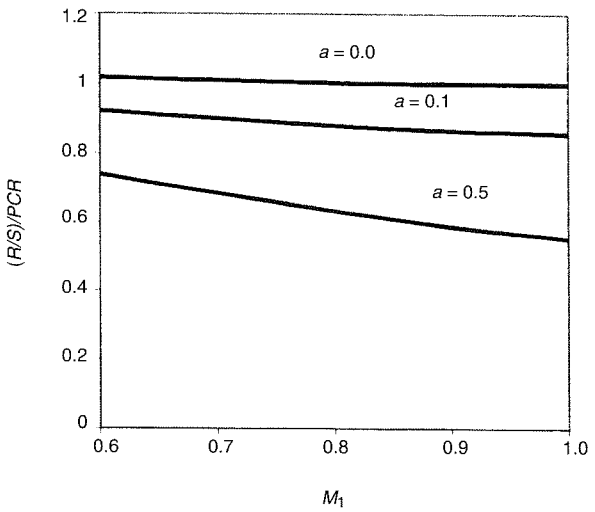
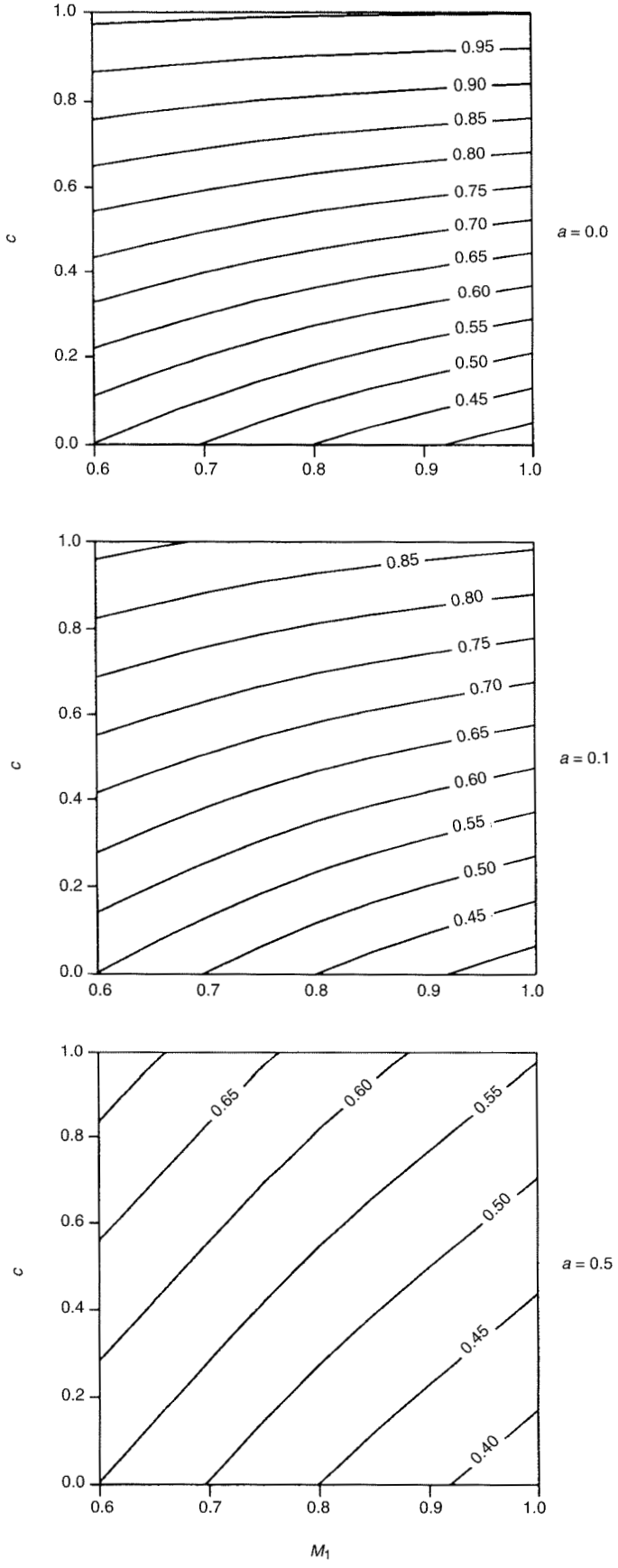


Figure 3: The ratio of *PCR* and *R/S* as a function of M_1 and a for an equilibrium population when $b = 100$ and $c = 1$, and M is assumed to be M_1.



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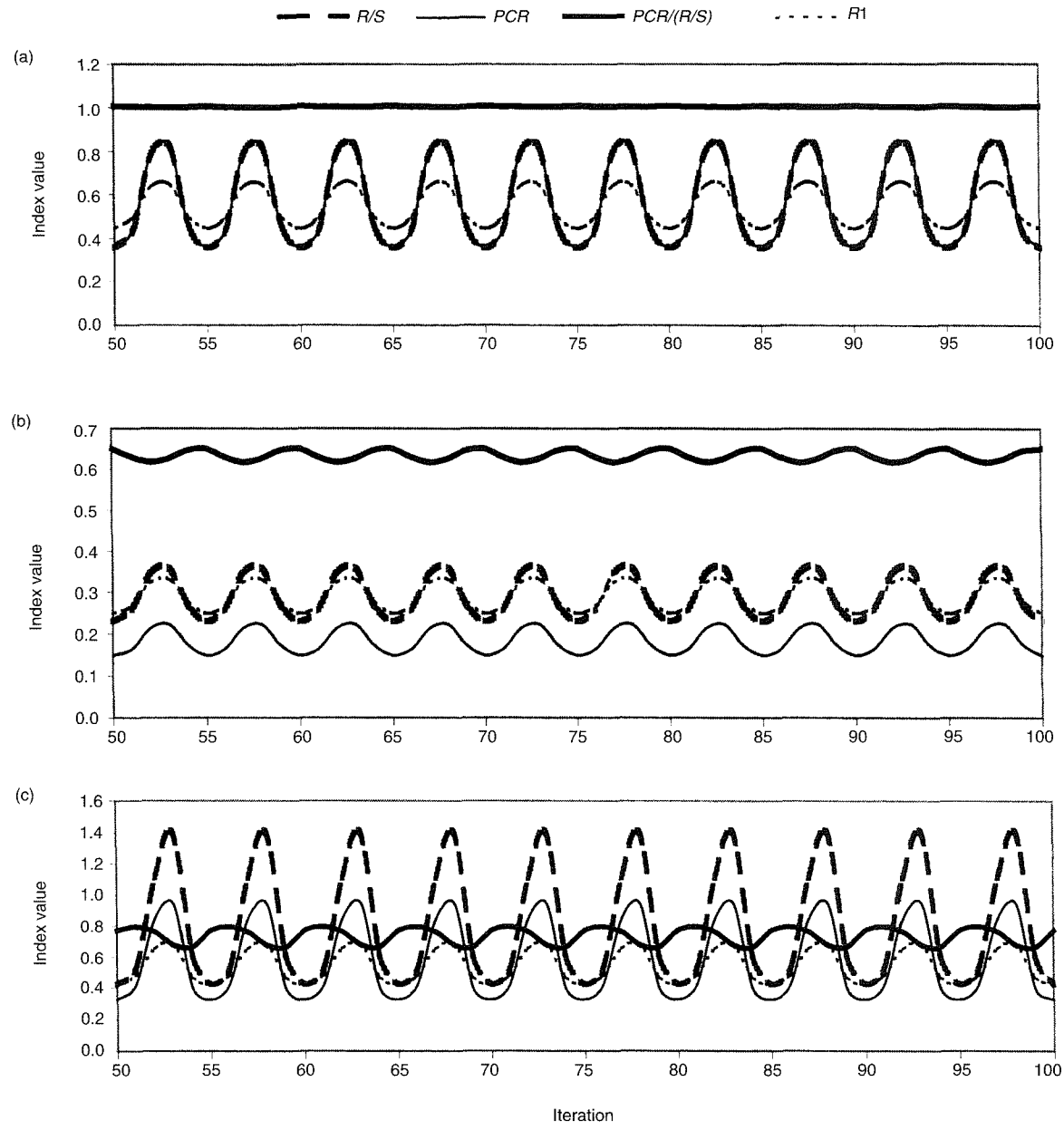


Figure 5: Variability of *R/S* (heavy dashed line), *R*1 (dotted line), *PCR* (solid line) and *PCR/(R/S)* (heavy solid line) over time as a response to introduced cycles in the relationship between spawners and recruits when: (a) $M_1 = 0.8$, $a = 0.0$ and $c = 1$; (b) $M_1 = 0.8$, $a = 0.5$ and $c = 1$; and (c) $M_1 = 0.8$, $a = 0.0$ and $c = 0.5$.

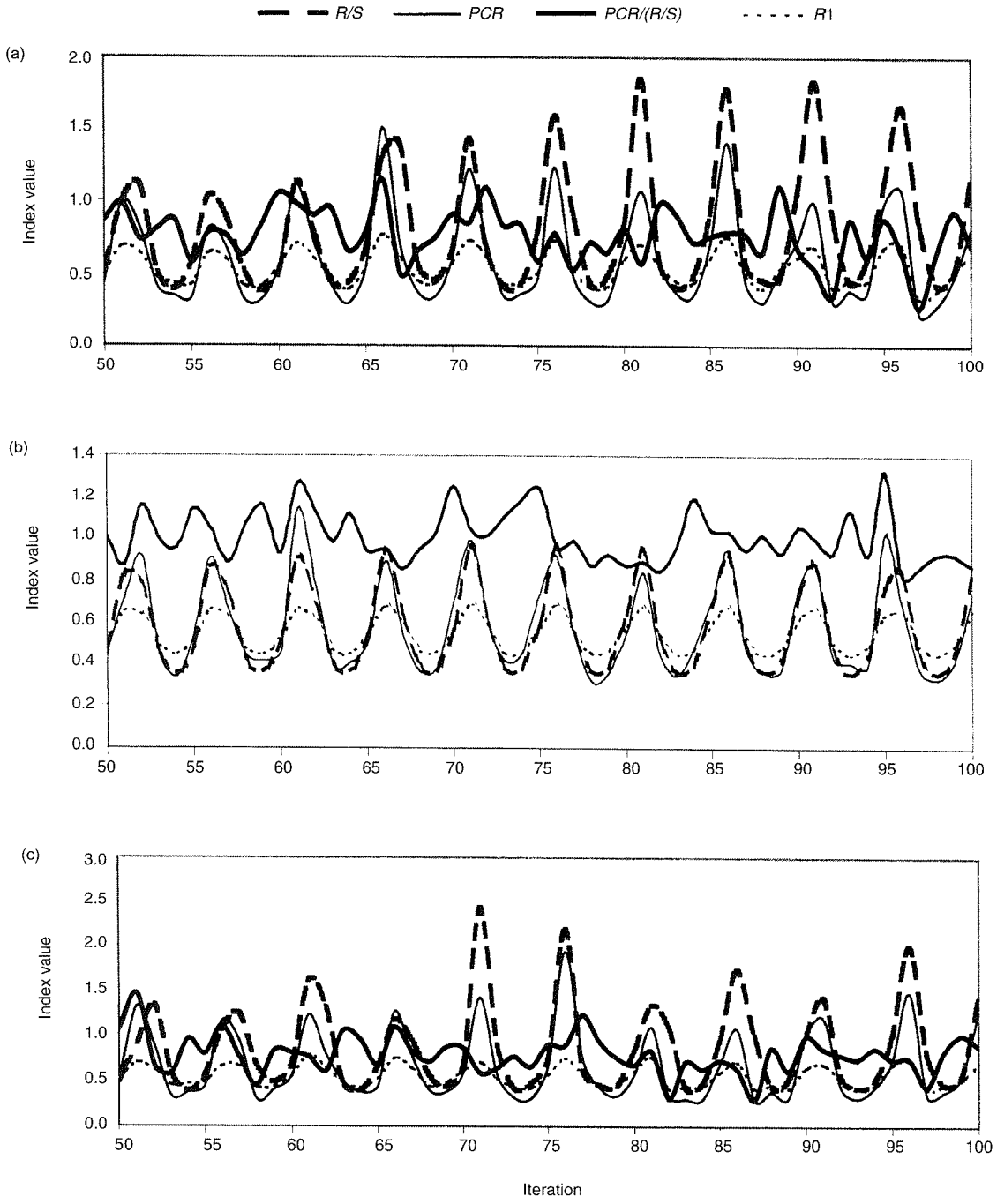
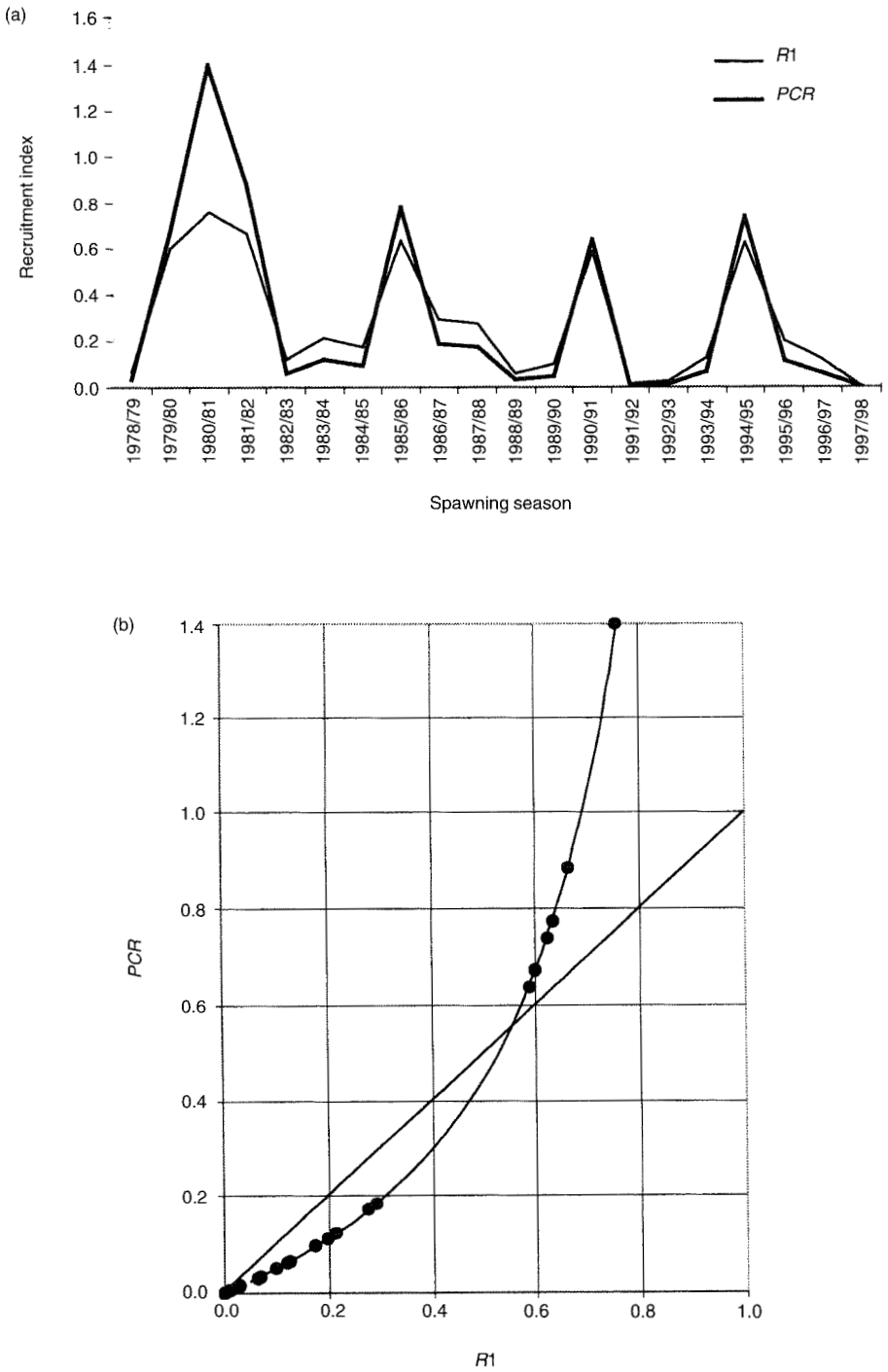


Figure 6: Variability of *R/S* (heavy dashed line), *R*1 (dotted line), *PCR* (solid line) and *PCR/(R/S)* (heavy solid line) over time as a response to introduced cycles in the relationship between spawners and recruits when: (a) $a = 0$, M_1 varies randomly between 0.6 and 1.0, and c varies randomly between 0 and 1; (b) $M_1 = 0.8$, $a = 0.0$, $c = 1$, and random sampling error added to the true value of *R*1 (±20%) prior to the calculation of *PCR*; and (c) when $a = 0.0$, M_1 varies randomly between 0.6 and 1.0, c varies randomly between 0 and 1, and random sampling error added to the true value of *R*1 (±20%) prior to the calculation of *PCR*.



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