Recruitment variability of Antarctic krill in Subarea 48.1 expressed as 'proportional recruitment': length threshold effects

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Abstract

Proportional recruitment summarises the variability of new individuals entering a population over time. Two parameters characterising proportional recruitment, the mean and standard deviation of the interannual proportion of juveniles in the population, are important inputs to the generalised yield model (Grym) when the proportional recruitment option is being used to set fishery catches. The Grym is a simulation framework that can define the amount of fisheries catch that is considered precautionary as defined by decision rules. It is currently under consideration by CCAMLR for managing catches of Antarctic krill. This study calculated proportional recruitment of krill from seven data sources in Subarea 48.1 representing research trawl surveys, fishery observer data and predator diets. Krill length-frequency distributions provided values of proportional recruitment from each of these data sources using a range of alternative upper length bounds ('thresholds') from 30 to 44 mm for defining juveniles. All datasets tracked the same interannual peaks and troughs in proportional recruitment. Proportional recruitment parameters calculated using the alternative thresholds from the same datasets varied widely. Across all data sources and thresholds, the interannual mean proportional recruitment of krill varied from 0.02 to 0.76 with standard deviations varying from 0.03 to 0.3. The choice of length threshold had a larger effect on the proportional recruitment parameters than differences among datasets. The potential importance of size selectivity in krill samples, especially if smaller bounds on the juvenile length threshold are assigned, could require adjusting observed frequencies for the lower selectivity of smaller individuals. These results highlight the importance of deciding which upper length bound and which data source(s) to use to identify juveniles in calculating the parameters to be supplied to the Grym.

Résumé

Le recrutement proportionnel représente la variabilité des nouveaux individus rejoignant une population au fil du temps. Deux paramètres qui caractérisent le recrutement proportionnel, à savoir la moyenne et l'écart-type de la proportion interannuelle de juvéniles dans la population, sont des données d'entrées importantes pour le modèle de rendement généralisé (Grym) lorsque l'option de recrutement proportionnel est utilisée pour établir les captures dans les pêcheries. Le Grym est une structure de simulation qui peut définir le niveau de captures dans les pêcheries considéré comme prudent en vertu des règles de décision. La CCAMLR l'envisage actuellement comme outil pour la gestion des captures de krill antarctique. Dans cette étude, le recrutement proportionnel du krill a été calculé d'après sept sources de données dans la sous-zone 48.1, provenant des campagnes de recherche par chalutages, des données d'observateurs des pêcheries et du régime alimentaire des prédateurs. La distribution des fréquences de taille du krill a fourni des valeurs de recrutement proportionnel pour chacune de ces sources de données en utilisant une série de bornes supérieures de longueur alternatives (« seuils ») entre 30 et 44 mm, afin de définir ce que sont les juvéniles. Tous les jeux de données ont détecté les mêmes pics et dépressions interannuels dans le recrutement proportionnel. Les paramètres de recrutement proportionnel calculés en utilisant les seuils alternatifs provenant des mêmes jeux de données varient largement. Sur l'ensemble des sources de données et des seuils, le recrutement proportionnel moyen interannuel de krill varie de 0,02 à 0,76, avec des écart-types allant de 0,03 à 0,3. Le choix du seuil de taille a eu plus d'effets sur les paramètres de recrutement proportionnel que les différences entre les jeux de données. L'importance possible de la sélectivité par taille dans les échantillons de krill, en particulier si des bornes plus petites sont assignées au seuil de longueur des juvéniles, pourrait nécessiter l'ajustement des fréquences observées pour la sélectivité plus basse des individus de plus petite taille. Ces résultats soulignent qu'il est important de décider quelle borne supérieure de longueur et quelle(s) source(s) de données(s) utiliser pour identifier les juvéniles dans les calculs des paramètres à fournir au Grym.

Абстракт

Пропорциональное пополнение обобщает изменчивость количества новых особей, поступающих в популяцию с течением времени. Два параметра, характеризующие пропорциональное пополнение, – среднее и стандартное отклонение межгодовой доли молоди в популяции – являются важными исходными данными для модели обобщенного вылова (Grym), когда вариант пропорционального пополнения используется для установления уловов. Grym – это система моделирования, позволяющая определить объем улова, который считается предохранительным в соответствии с правилами принятия решений. Данная система в настоящее время рассматривается АНТКОМ для управления промыслом антарктического криля. В данном исследовании пропорциональное пополнение криля рассчитывалось на основе семи источников данных из Подрайона 48.1, полученных исследовательскими траловыми съемками, данными наблюдателей промысла и из рационов хищников. Частотные распределения длины криля представили значения пропорционального пополнения по каждому из этих источников данных с использованием ряда альтернативных границ длины («порогов») от 30 до 44 мм для определения молоди. Все наборы данных отслеживали одни и те же межгодовые всплески и спады в пропорциональном пополнении. Параметры пропорционального пополнения, рассчитанные с использованием альтернативных пороговых значений из одних и тех же наборов данных, сильно различались. По всем источникам данных и пороговым значениям среднее межгодовое значение пропорционального пополнения криля варьировалось от 0,02 до 0,76 со стандартными отклонениями от 0,03 до 0,3. Выбор порога длины оказал большее влияние на параметры пропорционального пополнения, чем различия между наборами данных. Потенциальная важность размерной селективности в выборках криля, особенно при выборе меньших границ пороговой длины молоди, может потребовать корректировки наблюдаемых частот с учетом более низкой селективности мелких особей. Полученные результаты подчеркивают важность принятия решения о том, какую верхнюю границу длины и какие источники данных следует использовать для определения молоди при расчете параметров для Grym.

Resumen

El reclutamiento proporcional resume la variabilidad proporcional de los nuevos individuos que se unen a una población a lo largo del tiempo. Los dos parámetros que caracterizan el reclutamiento proporcional, la media y la desviación estándar de la proporción interanual de juveniles en la población, son contribuciones importantes para el modelo de rendimiento generalizado en R (Grym) cuando se utiliza la opción de reclutamiento proporcional para establecer las capturas pesqueras. El modelo Grym es una herramienta de simulación que puede definir la cantidad de captura pesquera que se considera precautoria según lo establecido por los criterios de decisión. Actualmente, el modelo se encuentra bajo consideración de la CCRVMA para ordenar las capturas de krill antártico. Este estudio calculó el reclutamiento proporcional de kril a partir de siete fuentes de datos en la Subárea 48.1, que representan prospecciones de arrastre, datos de observadores de pesca y dietas de depredadores. La distribución de la frecuencia de tallas de kril proporcionó valores de reclutamiento proporcional de cada una de estas fuentes de datos al utilizar un intervalo alternativo del límite superior de la talla ("umbrales") de 30 a 44 mm para definir a los juveniles. Todos los conjuntos de datos rastrearon los mismos puntos más altos y bajos interanuales en el reclutamiento proporcional. Los parámetros de reclutamiento proporcional calculados mediante el uso de valores umbrales alternativos de los mismos conjuntos de datos variaron ampliamente. A través de todas las fuentes de datos y valores umbrales, la media interanual del reclutamiento proporcional de kril varió entre un 0,02 a 0,76, con una desviación estándar que varió de un 0,03 a un 0,3. La elección del valor umbral de talla tuvo un efecto mayor sobre los parámetros de reclutamiento proporcional que las diferencias entre conjuntos de datos. La importancia de la selectividad por tallas en las muestras de kril, específicamente si se asignan límites más pequeños al valor umbral de talla de los juveniles, podría requerir el ajuste de las frecuencias observadas para la menor selectividad de los individuos más pequeños. Estos resultados destacan la importancia de definir qué límite superior de talla y qué fuente de datos se debería utilizar para identificar ejemplares juveniles en el cálculo de los parámetros a suministrarse en el modelo Grym.

Introduction

Recruitment, the annual production of individuals joining the pool of potentially reproductive members in a population, is highly variable in Antarctic krill (*Euphausia superba*) (Siegel and Loeb, 1995; Watkins, 1999; Siegel, 2000a; Siegel et al., 2002; Quetin and Ross, 2001, 2003; Kinzey et al., 2013, 2019). Recruitment parameters are important inputs to the generalised yield model (GYM), a modelling framework that makes future projections of krill abundance and variability under different levels of catch from a population determined by the model's input values (de la Mare, 1994a, 1994b; Constable and de la Mare, 1996). An R-version of the GYM (the Grym) has been developed (Maschette et al., 2020, 2021).[1] The effects of the different catches on the simulated population are compared in the Grym to CCAMLR decision rules (Constable et al., 2000), which define the amount of krill catch considered 'precautionary' based on the simulation results.

The GYM is a simulation model. Unlike statistical stock assessment models such as Casal2 (Bull et al., 2004), stock synthesis (Methot and Wetzel, 2013) or similar frameworks that formally quantify the uncertainty of model estimates by using a likelihood function (Hilborn and Mangel, 1997), simulation models do not quantify uncertainty. The likelihood function in statistical models compares model estimates to the data to assess the model 'fit' for candidate parameter estimates, whereas in simulation models all inputs are assumed known.

Quetin and Ross (2001) noted that the percentage of the krill population reproducing during the seven-year time series they studied in the Palmer Long-Term Ecological Research (LTER) study area from 1993 to 1999 varied from 10 to 98% annually, suggesting that immature individuals composed 2 to 90% of the standing stock in any given year. Quetin and Ross (2003) describe krill recruitment as 'episodic', suggesting that two strong year classes in succession are typically followed by three or four moderate or poor year classes. Similar patterns in year-class strength for krill have been observed in the Elephant Island region between 1976 and 1996 (Loeb et al., 1997). Krill under natural conditions can live five to eight years (Siegel, 2000b; Nicol, 2000), so the oldest age classes are largely a product of intermittent strong cohorts.

Recruitment can be represented using three separate options in the Grym: lognormal recruitment; a vector of absolute recruitment; or proportional recruitment. The option currently agreed upon by the Scientific Committee of CCAMLR for advising on management of the krill fishery is proportional recruitment.

Proportional recruitment represents the proportion of juveniles in the population and its variability, parameterised by specifying a mean and a standard deviation (SD). It is calculated as the interannual proportion of all individuals younger than, or equal to, a particular age class to all individuals in the population. The values of proportional recruitment have a large effect on the precautionary yield ('gamma', the proportion of unfished biomass, that can be harvested annually while meeting the CCAMLR decision rules) calculated using the outputs from the Grym. The proportional recruitment input values are largely responsible for the range of gamma values from 0 to 0.11 in the 36 scenarios reported in Table 5 of Maschette et al. (2021). For example, when the mean of proportional recruitment is 0.3 and the SD is 0.3 in a model otherwise configured as scenario 1 in Maschette et al. (2021), the precautionary gamma is 0, or no catch allowed by the decision rules. When the mean is 0.4 and

[1] https://github.com/ccamlr/Grym_Base_Case/tree/Simulations.

the SD is 0.3 in an otherwise similarly configured input file, the precautionary gamma is 0.04, 4% of unfished biomass (approximately 2.4 million tonnes catch given current estimates of krill biomass).

Juvenile krill have been identified for the GYM and Grym using several alternative approaches to define the juvenile life stage. These have been based either on estimated age ('R1' and 'R2' for ages 1 and 2 respectively), or directly from length data as the upper bound for juveniles (e.g. 'F35' or 'F40' for 35 or 40 mm krill). When krill ages are used as inputs, they are derived from length data that are assumed to be composed of mixtures of normal distributions of length at each age (e.g. Macdonald and Pitcher,1979; de la Mare, 1994a). There is no currently accepted method of aging krill directly.

A challenge to identifying juveniles by using a single length as an upper bound and then calculating a mean and SD for the frequency proportions at that bound is that krill actually mature over a range of lengths and ages, depending on local conditions such as ice coverage and chlorophyll density (Quetin and Ross, 2001; Brown et al., 2010; Kawaguchi, 2016). Female krill can begin spawning at age 2+ around the Antarctic Peninsula and age 3+ in the Antarctic Indian Ocean (Siegel and Loeb, 1994; Table 1 in Siegel, 2000b) but west of the Antarctic Peninsula krill usually do not reproduce until their fourth summer (Quetin and Ross, 2001). Males spawn a year later than females (Siegel, 2000b).

Reported catches of krill by the fishery from observer data during 2015–2020 have been predominately from CCAMLR Subarea 48.1 along the Antarctic Peninsula (49%) and Subarea 48.2 west of the South Orkney Islands (32%) (Table 3 in CCAMLR Fishery Report 2020). This study compares multiple indices of proportional recruitment calculated using different length thresholds separating juvenile and mature krill sampled from research trawl surveys, predator diets and the fishery in Subarea 48.1.

This study empirically tested the choice of length threshold on the input data values of proportional recruitment for krill in Subarea 48.1. The range of means and SD of proportional recruitment summarising complete length-frequency distributions that were obtained using multiple datasets of interannual krill length-frequencies are compared and contrasted. The potential effects of two types of selectivity are considered.

Methods and results

The mean and SD of proportional recruitment available for each data source were calculated separately by year and combined over all years. Proportional recruitment for each year y was the mean of the proportional recruitment in each sample $\overline{p}_y$ (each trawl in the surveys, or each lavage or spill sample around a juvenile feeding event by a penguin parent) collected during year y:

$$\overline{p}_y = \frac{\sum_1^s d_{st} / d_{sT}}{s_y} \tag{1}$$

where d_{st} is the sum of the numerical densities (for trawls) or counts (for predator diets) for the length bins ≤ the threshold length in sample s, d_{sT} is the sum of the numerical densities or counts for all length bins in sample s, and s_y is the number of samples collected in year y.

The mean of all years for each data source was:

$$\frac{\sum_y \overline{p}_y}{n_y} \tag{2}$$

where n_y is the number of years available for the data source.

Length frequencies for the fishery observer data were calculated as described by the CCAMLR Secretariat (2001), with additional vessel-specific catch weightings to account for differences among individual ships and between traditional and continuous trawls. Proportional recruitments from these fishery length-frequency distributions were then calculated for different length thresholds using equations (1) and (2) above.

Different length thresholds affected the value of d_{st} and hence $\sum_1^s d_{st} / d_{sT}$ in equation (1). The purpose of comparing proportional recruitment values derived from different thresholds is to illustrate the effect of the choice of juvenile maximum length on the Grym input parameters obtained.

Information sources for proportional recruitment

This study examined seven sources of data on krill length frequencies from Subarea 48.1 in January. These are the fishery observer data, two research trawl surveys and predator diets from four long-term studies of three penguin species. Most of these data sources were sampled for ≥20 years (Table 1). All data sources had multiple years with samples in January but not in other months. Comparing January samples allowed length frequencies to be compared among sources for the same month. The fishery length-frequency data were only available for eight years from 2011 to 2019 with no January samples in 2017. Proportional recruitments from the LTER trawl surveys from 2009 to 2019 extend an earlier time series of LTER trawl proportional recruitments from 1990 to 2011 reported in Figure 3b of Conroy et al., 2020. Although the time series in Table 1 depict different portions of the complete 31-year interval and different spatial regions of the Antarctic Peninsula (Figure 1), these seven time series are all long enough to sample at least one of the five- to six-year recruitment cycles proposed by Quetin and Ross (2003), even when they are not overlapping.

The point P in Figure 1 is the Palmer LTER station (Adélie penguins), CS is US AMLR Cape Shirreff station (chinstrap and gentoo penguins) and CP is US AMLR Copacabana station (chinstrap, gentoo and Adélie penguins). The Subarea 48.1 fishery is concentrated mostly to the south and north of the US AMLR stations. Not all predator and trawl stations were sampled every year.

The LTER diet dataset of Adélie penguins (*Pygoscelis adeliae*) had length bins ranging from 16.2 to 61.65 mm in 5.05 mm intervals. These were split into juveniles using the 1 mm threshold considered in the study by grouping all the LTER bins from the first bin (endpoints 16.2 and 21.25 mm) with all LTER bins that were less than, or equal to, the juvenile threshold.

Krill growth, maturity and alternative length thresholds

In recent parameterisations of the Grym, the period for krill growth is defined as 21 October to 12 February, with spawning occurring 15 December to 15 February (Appendix 1 in Maschette et al., 2021). A variety of krill lengths at maturity (the length range at which 50% of krill transform from juvenile to adult) in Area 48 was reported to SC-CAMLR working groups in 2021 (Table 2). These input maturity ranges provide a width and slope for ramp-shaped maturity inputs assigned to the population in the Grym. Different values for length at maturity will produce different parameterisations of proportional recruitment from the same length-frequency dataset because length at maturity defines the threshold between lengths that are considered juvenile and those considered mature.

A von Bertalanffy growth model connects the length-based maturity thresholds in Table 2 to krill ages as modelled in the Grym. In 2021, the von Bertalanffy parameters used to model krill growth in the Grym that predict mean length from age were modified from previous values of $L_\infty = 60.8$ and $k = 0.45$ used during WG-EMM-2010 to new values of $L_\infty = 60$ and $k = 0.48$ (Maschette et al., 2021).

The 2010 growth values were accompanied by a length range at 50% maturity from 32 to 42 mm whereas the 2021 growth values were accompanied by lengths at 50% maturity from 37.6 to 44.3 mm. Thus the 50% maturity range from 2021 is shifted to larger and older krill compared to the range from 2010 (Figure 2).

The means and SDs of proportional recruitment derived from seven datasets (Table 1) using five length thresholds (30, 35, 38, 40 and 44 mm) to separate juvenile and adult krill were calculated. These thresholds span the range of maximum lengths at 50% maturity reported in recent CCAMLR documents (Table 2).

Length-frequency distributions in AMLR trawl surveys and the fishery

The mean and SD of proportional recruitment summarise length-frequency distributions measured through time. Examination of the complete distributions can help understand the linkage between the length-frequency data and these summary parameters. The fishery observer data from January were shifted towards larger krill relative to the research trawls (Figure 3). The US AMLR trawl survey data displayed high densities of krill less than 30 mm in length for one or two years starting in 1992, 1996, 2002, 2007 and 2011 (Figure 3a).

Table 1: Data sources for krill January length-frequency distributions in Subarea 48.1 used in this study. N indicates the number of years measured and bin size indicates the units in which krill lengths were measured for each data source. US AMLR indicates the US Antarctic Marine Living Resources Program and Palmer LTER indicates the US Palmer Long-Term Ecological Research Program. Trawl data were converted to densities based on volume sampled. Proportional recruitments from the penguin data were calculated from the length-frequency ratios of krill in the diets each year.

Source	Years	N	Bin size (mm)
US AMLR trawl surveys	1991–2011	20	1
Palmer LTER trawl surveys[2]	2009–2019	11	1
CCAMLR fishery observer data	2011–2016, 2018–2019	8	2
US AMLR chinstrap diets	1993–2020	28	1
US AMLR gentoo diets	1993–2021	29	1
US AMLR Adélie penguin diets	1993–2022	30	1
Palmer LTER Adélie diets	1992–2018	27	5.05

[2] Palmer Station Antarctica LTER and Steinberg, 2020.

Table 2: CCAMLR documents reporting minimum and maximum krill lengths (mm) at 50% maturity and their range. Lengths are rounded to the nearest mm. Range is the total range of lengths over which some individuals are mature.

Authors	Reference	Min 50%	Max 50%	Range
Thanassekos et al., 2021	WG-SAM-2021/12 Figure 3	26	30	6
Maschette et al., 2020	SC-CAMLR-39/BG/19 Table 2	34	40	12
Maschette et al., 2021	WG-FSA-2021/39 Table 2 (2010)	32	37	6
Maschette et al., 2021	WG-FSA-2021/39 Table 2 (2021)	38	44	9

The fishery data collected very few individuals less than 30 mm (Figure 3b).

Proportional recruitment mean and SD for each data source

This study computed the mean and SD of proportional recruitment over all years available for each data source for both of the 30- and 44-mm thresholds (Figure 4 and Table 3). The fishery data for the standard trawl and continuous fishing systems were standardised and calculated by the CCAMLR Secretariat as described in WG-SAM-2021/07. The LTER and AMLR trawls were standardised for volume sampled and integrated over depth to produce density length-frequencies. The measured length frequencies from the predator data were used without being standardised for volume because the volume sampled by the predators was unknown.

The range of means and SD for proportional recruitment were lower when juveniles were defined as krill ≤30 mm (estimated age 1.4 years using the von Bertalanffy parameters considered here) than when juveniles were defined as krill ≤44 mm (estimated age 2.8 years). For the 30 mm threshold, the mean proportional recruitment ranged from 0.02 to 0.45, and the SD ranged from about 0.03 to 0.22 (Table 3). For the 44 mm threshold, the range of mean proportional recruitment was 0.48 to 0.76, and the range of SD increased to 0.2 to 0.3 (Table 3).

To further explore the effect of different juvenile threshold values on the mean and SD of proportional recruitment from these datasets, proportional recruitment was calculated at three additional juvenile length thresholds: 35, 38 and 40 mm, and the results plotted (Figure 5). Proportional recruitment increased as the length threshold for juveniles increased for all datasets (the plateau in the Palmer LTER Adélie penguin diet mean and SD from 38 to 40 mm is an artifact of the 5 mm bin size in that dataset). The SDs increased with the length threshold for gentoo penguins, chinstrap penguins, AMLR trawls and the fishery. The SDs peaked as thresholds increased and then decreased at the highest thresholds for Adélie penguins at both sites and for LTER trawls.

The fishery data started out with the lowest SDs of all the datasets at thresholds of 30 and 35 mm but had the highest SD of all the datasets by the 44 mm threshold. The low means and SDs at the smallest thresholds in the fishery samples were because these samples contained very few small krill (Figure 3b).

Seven time series of proportional recruitment

Evaluating interannual variations in proportional recruitment revealed useful information about recruitment variability in krill, especially when temporal patterns in the peaks and troughs of the annual values were compared among datasets (Figure 6). Research trawls and fishery samples have been separated from penguin diet samples in Figure 6 to better resolve the patterns for the individual data sources, but the peaks and troughs in proportional recruitment coincided in all seven datasets, indicating they were tracking the same variability in the time series of krill length frequencies in the population. However, there were consistent differences in the magnitude of annual proportional recruitment among the datasets. For example, annual proportional recruitments estimated from the fishery observer data were lower than those from Palmer LTER research trawls during the same years, especially for the 30 mm threshold (Figure 6a). Proportional recruitment computed from gentoo penguin diets generally had lower peak means than the means computed from other data sources for the same juvenile length threshold, while proportional recruitment from Adélie penguin diets in both the Palmer LTER and US AMLR samples generally had the highest peaks (Figure 6).

Discussion

Consistent with the findings of Quetin and Ross (2001) and Loeb et al. (1997), data collected by the US AMLR Program trawl surveys and penguin diets and LTER trawl surveys and penguin diets show strong recruitment events lasting over a two- or three-year period separated by periods of recruitment failure subsequently lasting approximately three years (e.g. Figures 3a and 6). Several of these cycles occur in the data, with peak proportions of recruits starting in 1992, 1996, 2002, 2007 and 2011. Cohorts resulting from such strong recruitment events can be followed for several years in the complete length-frequency distributions after most of these events.

The variability in recruitment expected over a 21-year projection period will likely be underestimated by datasets that span only a few years. The oscillating peaks and troughs of annual proportional recruitment in the seven datasets considered here required five or six years to track a single complete cycle (Figure 6).

Identifying which values for the mean and SD of proportional recruitment of krill to use in the Grym for calculating a precautionary yield has not been resolved by this study. Summarising time series of length-frequency distributions such as those evident in Figure 3 with a single mean and SD for each dataset discards potentially usable information in the krill length-frequency samples. As the length threshold separating juveniles and mature krill was reduced in this study, the mean and SD of proportional recruitment also decreased (Figure 4). This was particularly noticeable for datasets such as the fishery length frequencies, which had the lowest SD for proportional recruitment of the seven datasets at a 30 mm threshold (0.022) but the highest SD at a 44 mm threshold (0.3).

The differences in the smallest krill obtained in the research trawl and fishery samples indicate different length selectivity patterns for research trawls and the fishery (Figure 3). Differences in selectivity were also apparent in the penguin data, where gentoo penguins usually had lower peaks in proportional recruitment than Adélie penguins and chinstrap penguins were intermediate (Figures 4 and 5).

Sample selectivity can be separated into two processes, 'target' (sometimes called 'gear') selectivity (the samples have differing probabilities of capturing different sizes of krill that are present in the regions sampled) and 'availability' (krill of specific sizes in the population do not occur in the region being sampled) (Crone et al., 2014; Punt et al., 2013; Kinzey et al., 2015). Both types of selectivity can act jointly to affect length-frequency distributions observed at a particular place and time. Since all large krill were once smaller krill, if small

Table 3: Mean and SD of proportional recruitment for the seven data sets when the juvenile length threshold is 30 and 44 mm. Data source names as for Figure 4. Proportional recruitment parameters from the combined AMLR and LTER trawl datasets are labelled as amlr&lter.trwl. Lengths from the combined US AMLR penguin species diets are amlr.peng.all (krill lengths from LTER Adélie penguin diets were measured in units of 5 mm so were not combined with the 1 mm binned US AMLR samples).

Sources	Threshold 30mm		Threshold 44mm	
	Mean	SD	Mean	SD
gepeng	0.024	0.035	0.511	0.222
chpeng	0.033	0.037	0.581	0.249
adpeng	0.068	0.078	0.72	0.213
adpeng.LTER	0.09	0.078	0.685	0.258
fsh.481	0.022	0.022	0.542	0.3
amlr.trwl	0.154	0.122	0.481	0.218
lter.trwl	0.449	0.224	0.764	0.196
amlr&lter.trwl	0.259	0.217	0.582	0.249
amlr.peng.all	0.038	0.04	0.576	0.228

krill do not occur in a sample dataset in sufficient proportions to supply the observed cohort abundances of older individuals, at least one of these two types of selectivity must be occurring.

As already noted, the fishery catches few krill <30 mm in length (Figure 3b), so juvenile/mature length boundaries near 30 mm should not be expected to track recruitment in the fishery samples unless low selectivity for smaller individuals is accounted for. Gear selectivity by commercial trawls has been estimated to be about 0.25 for 30 mm krill, about 0.75 for 35 mm krill and increasing steeply for krill <30 mm (Figure 8 in Krag et al., 2014). Dividing the original counts in the observer samples by selectivity-at-length to correct for gear selectivity's effect on the observed length frequencies would increase 30 mm krill fourfold and 35 mm krill by a 1.33 multiplier in the local krill length frequencies being sampled by the trawls. Dividing the numbers of all krill at length in the samples by their selectivities would correct for gear selectivity. However, this would not address the availability component of selectivity if the fishery samples were obtained from locations biased toward krill of particular sizes.

An appropriate length threshold to use for representing juveniles could possibly be selected using maturity data such as are routinely collected during trawl surveys (Reiss, 2016). Such thresholds would likely be at the smaller krill lengths that are under-represented due to selectivity, making correcting the samples for selectivity increasingly important as the length at maturity in the Grym is reduced. The research surveys sampled a stationary grid over many years regardless of krill density at each station while the fishery targets areas of high density and sizes/stages that are best for processing. Adding a fixed series of randomly selected stations in the future to measure length distributions by the fishery before fishing commences could reduce the selectivity of using data from targeted catches to represent the population.

Conclusions

Capturing the complexities of krill recruitment dynamics using the mean and SD of the proportion of individuals sampled smaller than a single length threshold is a challenge. Various thresholds for the length boundary between juvenile and mature krill have been proposed. This study demonstrated that a wide range of proportional recruitment parameters are obtainable from different assumptions about the length threshold separating juveniles and mature krill in length-frequency sampling data. Which of these thresholds is actually used to calculate the inputs to the Grym will have a large impact on the precautionary yield that is obtained (e.g. Table 5 in Maschette et al., 2021). As the length threshold separating juveniles and adults decreased, the mean and SD of proportional recruitment calculated from a particular data source also decreased. However, smaller individuals have lower selectivities than larger krill for most or all of the sampling approaches (i.e. research trawls, commercial trawls and penguin diets) considered here, so as the threshold separating juveniles and adults decreases, the importance of selectivity under-representing small krill increases.

Estimates regarding krill population dynamics using proportional recruitment might be improved by analytical methods not used in this study. The effect of selectivity on estimating proportional recruitment in any given year can be addressed by dividing the observed numbers of small individuals in a length-frequency distribution by the length-specific selectivity of the given sampling approach before calculating proportional recruitment.

The current Grym simulation of the krill stock requires the proportional recruitment to be a single distribution of proportional recruitments with the same mean and SD. Although separate simulations of trials with proportional recruitment randomly selected from different length-frequency distributions may be modelled, there is currently no way to model proportional recruitments stemming from a range of maturity thresholds in a single set of trials in the Grym.

Modelling ranges in the mean and SD of proportional recruitment associated with different lengths at maturity instead of using a single length threshold could potentially be addressed by supplying a different proportional recruitment mean ($\overline{R}_t$) and standard deviation (σ_t) for each trial *t*. These trial-specific values could be obtained using a single random draw from a uniform distribution between the minimum and maximum values of plausible single length thresholds (equation (3)), but this would need to be implemented in the code and the ranges of mean and SD values to use would need to be identified:

$$\begin{aligned} \overline{R}_t &\sim U\left(\min(\overline{R}), \max(\overline{R})\right), \\ \sigma_t &\sim U\left(\min(\sigma), \max(\sigma)\right) \end{aligned} \tag{3}$$

where the minimum and maximum $\overline{R}$ and σ bounds are obtained from empirical studies.

A final point is that proportional recruitment is not the only way to model recruitment. The Grym itself has two other options for recruitment, lognormal and a vector of abundances option. Whether any of these three Grym options are capable of representing the actual patterns of recruitment that are evident in the length-frequency data, exhibiting correlations among strong recruitment years and intermittent years of recruitment failure, is arguable. Other options exist for modelling the complete length-frequency distributions of recruitment through time, such as fitting length-frequency data to a multinomial or a Dirichlet distribution (e.g. Candy, 2008). Using a statistical modelling framework (e.g. Bull et al., 2004; Methot and Wetzel, 2013; Doonan et al., 2015; Kinzey et al., 2018) in which a likelihood function connects the model and data, instead of simulation modelling where model inputs are treated as known quantities, is also possible, but such alternatives are beyond the scope of this paper.

Data and code availability

The datasets and R-scripts used to produce the results reported in this paper are available at https://github.com/us-amlr/krill-proportional-recruitment.

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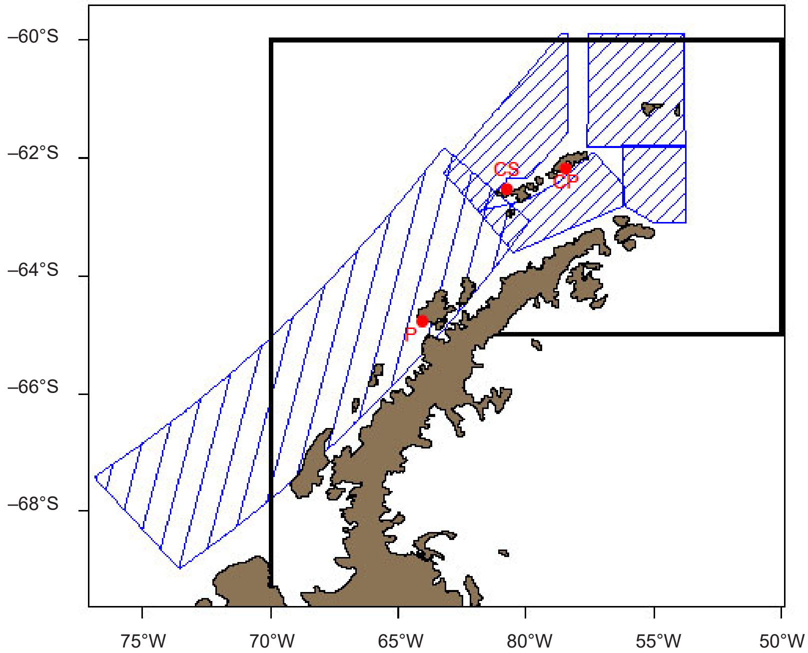

Figure 1: Approximate sampling locations of the seven data sources on interannual variability of krill length-frequencies northwest of the Antarctic Peninsula. Subarea 48.1 boundaries indicated by black lines. Hatched blue boxes enclose the US AMLR trawl survey locations (four boxes around and northeast of 'CS and 'CP') and the LTER trawl survey locations (box around 'P').

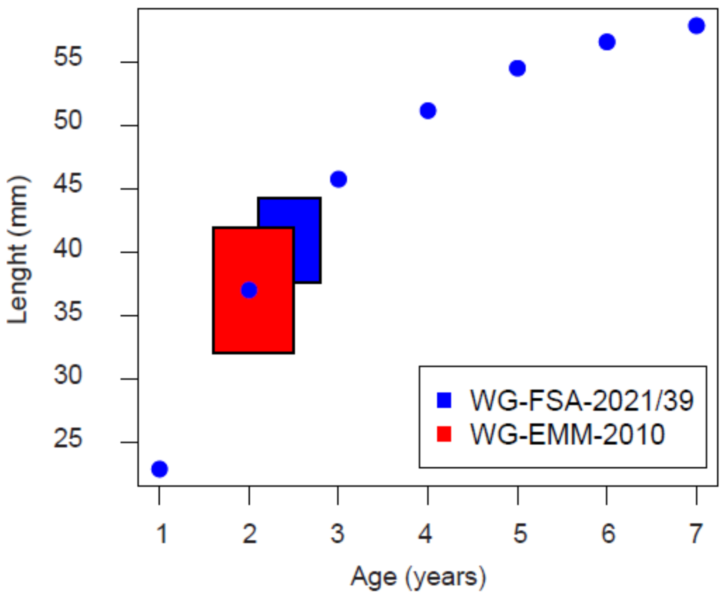

Figure 2: Krill von Bertalanffy length at ages 1 to 7 (blue points), as used in a recent parameterisation of the Grym, on 1 November for $L_\infty = 60$ mm and $k = 0.48$. The length and age ranges for 50% maturity for the parameterisation used in 2010 (red box) and in 2021 (blue box) are shown for comparison.

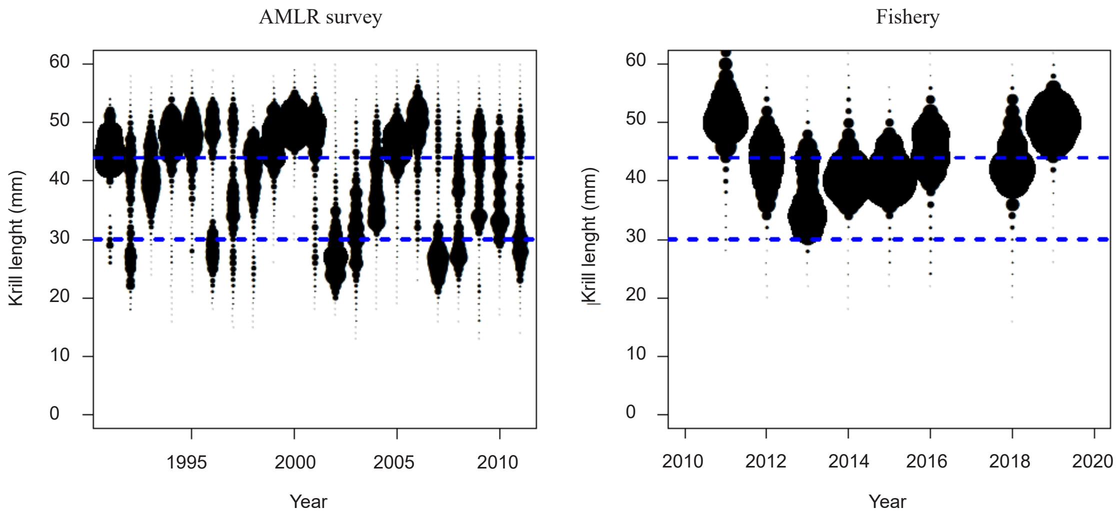

Figure 3: Length-frequency proportions for krill from: (a) US AMLR research trawls (January 1991 to 2011), and (b) fishery observer samples (January, 2011 to 2019). Blue dashed horizontal lines at 30 and 44 mm indicate the outer boundaries of the length thresholds used for computing the mean and SD of proportional recruitment. The proportions in each year sum to one.

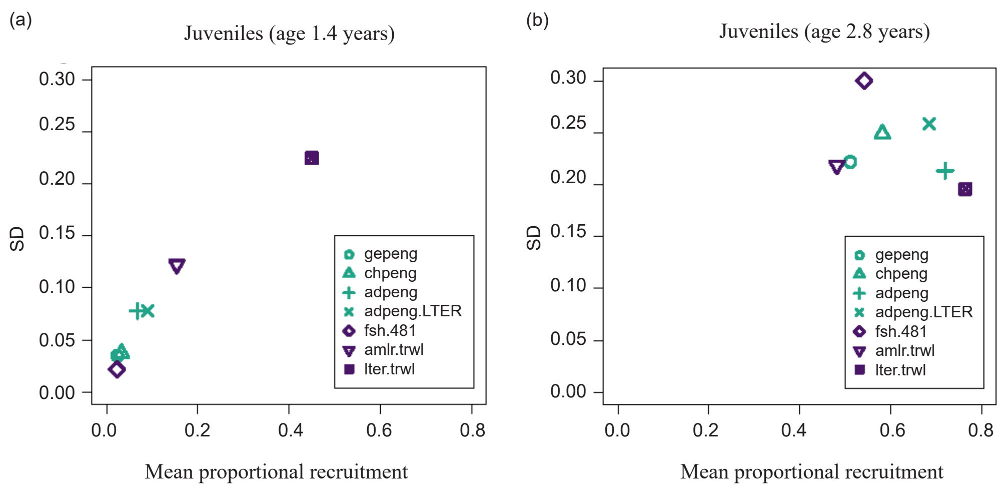

Figure 4: Proportional recruitment annual means (x-axis) and SDs (y-axis) for the seven January data sources (Table 1) when: (a) juveniles are defined as ≤30 mm, and (b) juveniles are defined as ≤44 mm. Legend definitions: gepeng = gentoo penguin diets sampled by the US AMLR Program; chpeng = chinstrap penguin diets sampled by the US AMLR Program; adpeng = Adélie penguin diets sampled by the US AMLR Program; adpeng.LTER = Adélie penguin diets sampled by the Palmer LTER; fsh.481 = fishery observer data; amlr.trwl = research trawl data collected by the US AMLR Program; lter.trwl = research trawl data collected by the Palmer LTER.

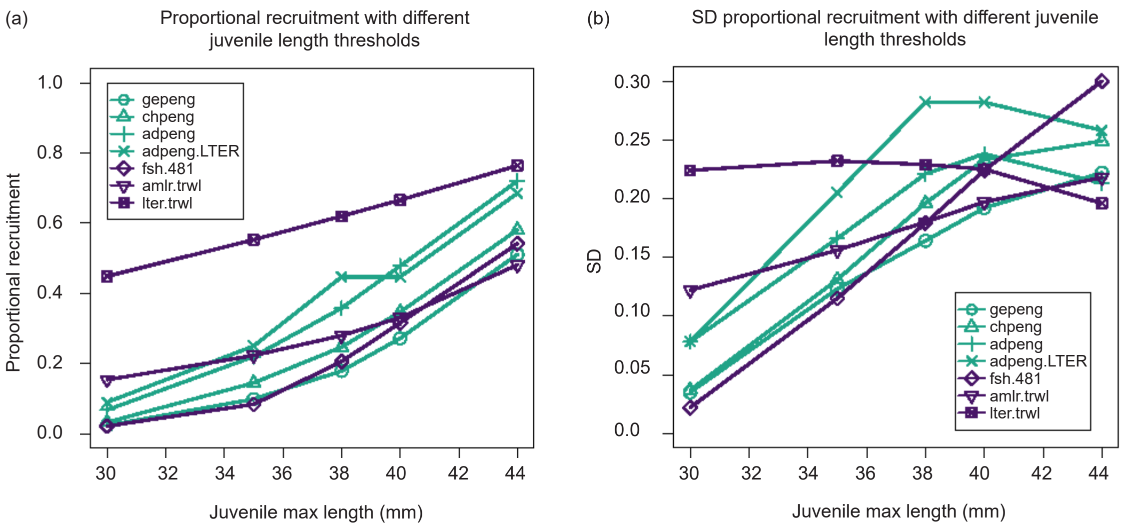

Figure 5: Proportional recruitment interannual: (a) mean, and (b) SD for the seven datasets at five different length thresholds separating juvenile and mature krill. Legend definitions are as for Figure 4.

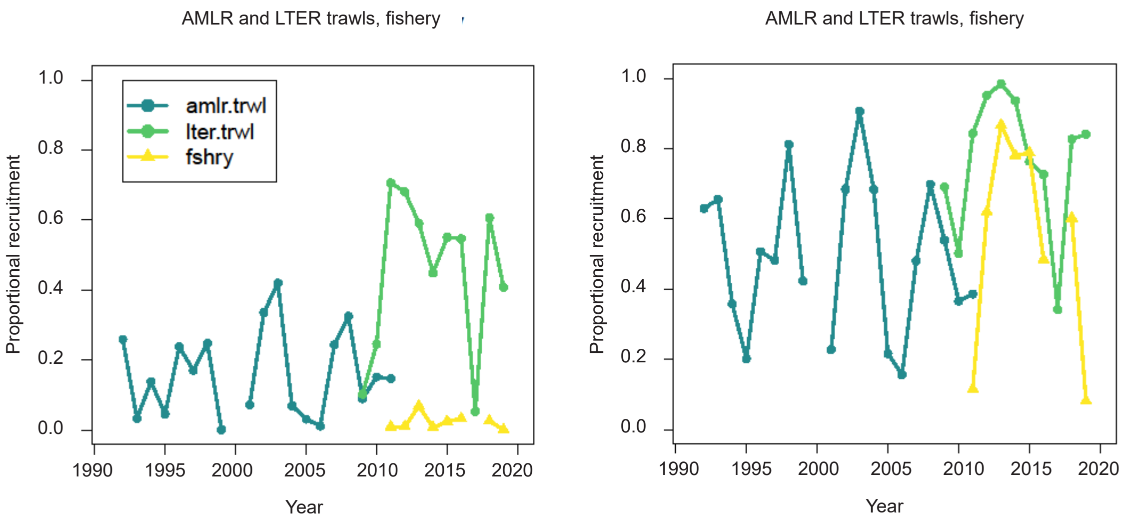

Figure 6: Time series of proportional recruitment from research trawls conducted by the US AMLR (amlr.trwl) and Palmer LTER (lter.trwl) programs and the fishery with juvenile krill (top panels) and from four penguin diet datasets with juvenile krill defined as (a) ≤30 mm, and (b) ≤44 mm.

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Tableau 1 : Sources de données sur la distribution des fréquences de taille du krill en janvier dans la sous-zone 48.1 utilisées dans cette étude. N indique le nombre d'années mesurées et fréquence d'émission (*bin size*) indique les unités dans lesquelles les longueurs de krill ont été mesurées pour chaque source de données. US AMLR désigne le programme des États-Unis sur les ressources marines vivantes de l'Antarctique et Palmer LTER désigne le programme de recherche écologique à long terme des États-Unis. Les données de chalutage ont été converties en densités en fonction du volume échantillonné. Le recrutement proportionnel issu des données sur les manchots a été calculé à partir des ratios de fréquence de taille du krill présents dans leur régime alimentaire chaque année.

Tableau 2 : Liste des documents de la CCAMLR présentant les tailles minimales et maximales de krill (mm) à 50 % de maturité et leur amplitude (*range*). Les tailles sont arrondies au mm le plus proche. Par amplitude, on entend l'amplitude totale des tailles auxquelles les individus sont matures.

Tableau 3 : Moyenne et écart-type du recrutement proportionnel pour les jeux de données lorsque le seuil des tailles des juvéniles se trouve entre 30 et 44 mm. Voir figure 4 pour les noms des sources de données. Les paramètres de recrutement proportionnel issus des jeux de données combinés des chaluts de l'AMLR et du LTER sont libellés « amlr&lter.trwl ». Les tailles issues des régimes alimentaires combinés des espèces de manchots de l'US AMLR sont libellées « amlr.peng.all » (les tailles du krill issu du régime alimentaire des manchots Adélie du LTER ont été mesurées en unités de 5 mm et n'ont pas été combinées avec les lots de taille de 1 mm échantillonnés par l'US AMLR).

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Figure 1 : Lieux approximatifs d'échantillonnage des sept sources de données sur la variabilité interannuelle des données de fréquence de tailles au nord-ouest de la péninsule antarctique. Les limites de la sous-zone 48.1 sont indiquées par des lignes noires. Les cases bleues hachurées représentent les emplacements des campagnes d'évaluation par chalutage de l'US AMLR (les quatre cases autour et au nord-est de « CS » et « CP ») et les emplacements des campagnes d'évaluation par chalutage du LTER (la case entourant « P »).

Figure 2 : Taille par âge de von Bertalanffy du krill de 1 à 7 ans (points bleus), tel qu'utilisé dans une paramétrisation récente du Grym, le 1er novembre pour L_∞ = 60 mm et k = 0,48. L'amplitude des tailles et des âges à 50 % de maturité pour la paramétrisation utilisée en 2010 (case rouge) et en 2021 (case bleue) servent de point de comparaison.

Figure 3 : Proportions des fréquences de taille du krill issues : a) des chaluts de recherche de l'US AMLR (janvier, de 1991 à 2011), et b) des échantillons d'observateurs des pêcheries (janvier, de 2011 à 2019). Les lignes horizontales en pointillés bleus à 30 et 44 mm indiquent les limites extérieures des seuils de taille utilisés pour le calcul de la moyenne et de l'écart-type du recrutement proportionnel. Les proportions pour chaque année sont égales à un.

Figure 4 : Moyennes (abscisse) et écart-types (ordonnée) annuels du recrutement proportionnel pour les sept sources de données de janvier (tableau 1) lorsque : a) les juvéniles sont définis comme mesurant ≤ 30 mm, et b) les juvéniles sont définis comme mesurant ≤ 44 mm. Explication des légendes : gepeng = régime alimentaire des manchots papou échantillonné dans le cadre du programme US AMLR ; chpeng = régime alimentaire des manchots à jugulaire échantillonné dans le cadre du programme US AMLR ; adpeng = régime alimentaire des manchots Adélie échantillonné dans le cadre du programme US AMLR ; adpeng.LTER = régime alimentaire des manchots Adélie échantillonné le cadre du programme Palmer LTER ; fsh.481 = données d'observateurs des pêcheries ; amlr.trwl = données de recherches par chalutage collectées dans le cadre du programme US AMLR ; lter.trwl = données de recherches par chalutage collectées dans le cadre du programme Palmer LTER.

Figure 5 : Recrutement proportionnel interannuel : a) moyenne, et b) écart-type pour les sept jeux de données à cinq seuils de taille différents en séparant les juvéniles et le krill mature. Voir figure 4 pour l'explication des légendes.

Figure 6 : Série chronologique de recrutement proportionnel issue des chaluts de recherche du programme US AMLR (amlr.trwl) et du programme Palmer LTER (lter.trwl), de la pêcherie contenant des juvéniles de krill (en haut) et des jeux de données sur le régime alimentaire de manchots, les juvéniles de krill étant définis comme mesurant a) ≤ 30 mm, et b) ≤ 44 mm.

Список таблиц

Табл. 1: Источники данных по январским частотным распределениям длины криля в Подрайоне 48.1, использованные в данном исследовании. N указывает на количество лет проведения измерений, а размер бина – на единицы измерения длины криля для каждого источника данных. США AMLR означает Программу морских живых ресурсов Антарктики США, а Palmer LTER – Программу долгосрочных экологических исследований США Palmer. Данные траления были преобразованы в плотность на основе объема отобранных проб. Пропорциональная численность рекрутов по данным исследований пингвинов была рассчитана на основе соотношения длины и частоты криля в составе рационов за каждый год.

Табл. 2: Документы АНТКОМ, в которых указаны минимальная и максимальная длина криля (мм) при 50%-ной зрелости и их диапазон. Длина округляется до ближайшего мм. Диапазон – это общий диапазон длин, в котором некоторые особи являются зрелыми.

Табл. 3: Среднее и стандартное отклонение пропорционального пополнения для семи наборов данных, в которых порог длины молоди составляет 30 и 44 мм. Названия источников данных как к Рис. 4. Параметры пропорционального пополнения из объединенных траловых наборов данных AMLR и LTER обозначены как amlr&lter.trwl. Длина криля из объединенного набора данных по данным исследований пингвинов США AMLR обозначена как amlr.peng.all (длина криля из набора данных по пингвинам Адели LTER измерялась в единицах по 5 мм, поэтому не была объединена с образцами США AMLR, которые измерялись с точностью до 1 мм).

Список рисунков

Рис. 1: Приблизительные места отбора проб из семи источников данных о межгодовой изменчивости частот длины криля к северо-западу от Антарктического полуострова. Границы Подрайона 48.1 обозначены черными линиями. Заштрихованными синими квадратами отмечены места траловых съемок США AMLR (четыре квадрата вокруг и к северо-востоку от «CS» и «CP») и места траловых съемок LTER (квадрат вокруг «P»).

Рис. 2: Длина криля по фон Берталанфи в возрасте от 1 до 7 лет (синие точки), которая использовалась в недавней (1 ноября) параметризации Grym для L_∞=60 мм и k=0,48. Для сравнения показаны диапазоны длины и возраста 50%-ной зрелости для параметризации, использованной в 2010 г. (красная рамка) и в 2021 г. (синяя рамка).

Рис. 3: Пропорции частоты длины для криля из: (a) исследовательских тралений США AMLR (январь, 1991–2011 гг.) и (b) выборок наблюдателей (январь, 2011–2019 гг.). Синие пунктирные горизонтальные линии на уровнях 30 и 44 мм обозначают внешние границы пороговых значений длины, используемых для расчета средних значений и стандартного отклонения пропорционального набора. Пропорции в каждом году равны единице.

Рис. 4: Пропорциональные годовые значения пополнения (ось x) и стандартное отклонение (ось y) для семи январских источников данных (Табл. 1), в случае, когда: (a) молодь определяется как ≤30 мм, и (b) молодь определяется как ≤44 мм. Условные обозначения: gepeng = рацион папуасских пингвинов, отобранный в рамках Программы США AMLR; chpeng = рацион антарктических пингвинов, отобранный в рамках Программы США AMLR; adpeng = рацион пингвинов Адели, отобранный в рамках Программы США AMLR; adpeng.LTER = рацион пингвинов Адели, отобранный в рамках Palmer LTER; fsh.481 = данные наблюдателей промысла; amlr.trwl = данные исследовательского траления, полученные в рамках программы США AMLR; lter.trwl = данные исследовательского траления, полученные Palmer LTER.

Рис. 5: Пропорциональное пополнение в межгодовой период: (a) среднее значение и (b) стандартное отклонение для семи наборов данных при пяти различных пороговых значениях длины, отличающих молодь криля от зрелых особей. Условные обозначения как к Рис. 4.

Рис. 6: Временные ряды пропорционального пополнения из исследовательских тралений, проводимых программами США AMLR (amlr.trwl) и Palmer LTER (lter.trwl) и промысла с включением молоди криля (верхние панели), а также из четырех наборов данных по рациону пингвинов с включением молоди криля, определенного как (a) ≤30 мм и (b) ≤44 мм.

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Tabla 1: Fuentes de datos utilizadas en enero para las distribuciones de frecuencia de tallas de kril en la Subárea 48.1. N indica el número de años que se midieron y el conjunto de intervalos (*bin size*) indica las unidades en que las tallas de kril se midieron para cada fuente de datos. El acrónimo 'US AMLR' se refiere al Programa de los EE. UU. sobre los Recursos Vivos Marinos Antárticos, mientras que 'Palmer LTER' se refiere al Programa de los EE. UU sobre Investigaciones Ecológicas a Largo Plazo. Los datos de los artes de arrastre se convirtieron en densidades basadas en el volumen muestreado. Los reclutamientos proporcionales basados en los datos de pingüinos se calcularon se calcularon a partir de las relaciones talla-frecuencia de kril en las dietas de cada año.

Tabla 2: Documentos de la CCRVMA que informan las tallas mínimas y máximas de kril (mm) al 50 % de madurez y su respectivo intervalo. Se redondean las tallas a los mm más próximos. El rango (*range*) es el intervalo total de tallas en las que algunos individuos se consideran maduros.

Tabla 3: La media y la desviación estándar del reclutamiento proporcional para 7 conjuntos de datos cuando el valor umbral de talla para juveniles es de 30 y 44 mm. Nombres de fuentes de datos como se detalla en la Figura 4. Los parámetros del reclutamiento proporcional de los conjuntos de datos de los artes de arrastre de las prospecciones US AMLR y LTER combinados se referencian como 'amlr&lter.trwl'. Las tallas de las dietas combinadas de las especies de pingüinos (US AMLR) se referencian como 'amlr.peng.all' (tallas de kril provenientes de las dietas de los pingüinos Adelia (LTER) se midieron en unidades de 5 mm, por lo que no se combinaron con las muestras US AMLR categorizadas en intervalos de 1 mm).

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Figura 1: Lugares aproximados de muestreo de las siete fuentes de datos sobre la variabilidad interanual de las frecuencias de talla del kril al noroeste de la península Antártica. Los límites de la Subárea 48.1 se indican con líneas negras. Los recuadros azules sombreados encierran las ubicaciones de la prospección de arrastre US AMLR (cuatro casillas alrededor y al noreste de 'CS' y 'CP') y las ubicaciones geográficas de la prospección de arrastre LTER (casilla alrededor de 'P').

Figura 2: Talla del kril en las edades de 1 a 7 según el modelo de von Bertalanffy (puntos azules), tal y como se usó recientemente (1 de noviembre) en una determinación de parámetros de Grym para L_∞ = 60 mm y k = 0.48. A título comparativo, se muestran los intervalos de talla y edad para el 50 % de madurez para la determinación de parámetros utilizada en 2010 (recuadro rojo) y en 2021 (recuadro azul).

Figura 3: Proporciones de frecuencia de talla para kril de: (a) prospecciones de investigación US AMLR (enero, 1991 a 2011), y (b) muestreo del observador de pesca (enero, 2011 a 2019). Las líneas azules horizontales discontinuas en 30 mm y 44 mm indican los límites exteriores de los valores umbrales de talla utilizados para calcular la media y la desviación estándar del reclutamiento proporcional. Las proporciones de cada año suman uno.

Figura 4: Media del reclutamiento proporcional anual (x-axis) y la desviación estándar (y-axis) para las siete fuentes de datos de enero (Tabla 1) cuando: (a) se definió a los ejemplares juveniles como ≤30 mm, y (b) se definió a los ejemplares juveniles como ≤44 mm. Definiciones de las referencias: **gepeng** = dieta del pingüino papúa muestreada por el programa US AMLR; **chpeng** = dieta del pingüino de barbijo muestreada por el programa US AMLR;

adpeng = dieta del pingüino Adelia muestreada por el programa US AMLR; **adpeng.LTER** = dieta del pingüino Adelia muestreada por el programa Palmer LTER; **fsh.481** = datos de los observadores de pesca; **amlr.trwl** = datos de los artes de arrastre de investigación recabados por el programa US AMLR; **lter.trwl** = artes de arrastre de investigación recabados por el programa Palmer LTER.

Figura 5: Reclutamiento proporcional interanual: (a) media; y (b) desviación estándar para los siete conjuntos de datos en cinco valores umbrales de talla diferentes que separan a los ejemplares juveniles de kril de los maduros. Las definiciones de las referencias son las que se detallan en la Figura 4.

Figura 6: Serie temporal del reclutamiento proporcional de los artes de arrastre de investigación recabados por el programa US AMLR (amlr.trwl) y por el programa Palmer LTER (lter.trwl) y de las pesquerías con ejemplares juveniles de kril (panel superior) y de cuatro conjuntos de datos sobre la dieta de los pingüinos con ejemplares juveniles de kril que se definen como (a) ≤30 mm, y (b) ≤44 mm.