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From land to ocean: one month for southern elephant seal pups to acquire aquatic skills prior to their first departure to sea

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Highlights

- During the on-land post-weaning period, the time spent resting decreases and an increasing proportion of physical activity shifts from land to shore.
- The leanest weanlings are active earlier and to a greater degree than their corpulent congeners.
- During the post-weaning period, a clear circadian activity with two peaks at dawn and dusk is observed.
- Pups on Kerguelen rarely dive and never deeper than a few meters prior to their first at-sea foraging trip.

Abstract

Weaned southern elephant seals (SES) quickly transition from terrestrial to aquatic life after a 5- to 6-week post-weaning period. At sea, juveniles and adult elephant seals present extreme, continuous diving behaviour. Previous studies have highlighted the importance of the post-weaning period for weanlings to prepare for the physiological challenges of their future sea life. However, very little is known about how their body condition during this period may influence the development of their behaviour and brain activities. To characterise changes in the behavioural and brain activity of weanlings prior to ocean departure, we implemented a multi-logger approach combining measurements of movements (related to behaviour), pressure (related to diving), and brain electrical activity. As pups age, the amount of time allocated to resting decreases in favour of physical activity. Most resting (9.6 ± 1.2 h/day) takes place during daytime, with periods of slow-wave sleep representing 4.9 ± 0.9 h/day during the first 2 weeks. Furthermore, an increasing proportion of physical activity transitions from land to shore. Additionally, pups in poorer condition (lean group) are more active earlier than those in better condition (corpulent group). Finally, at weaning, clear circadian activity with two peaks at dawn and dusk is observed, and this pattern remains unchanged during the 4 weeks on land. This circadian pattern matches the one observed in adults at sea, with more prey catches at dawn and dusk, raising the question of whether it is endogenous or triggered by the mother during lactation.

Keywords (3-6)

Mirounga leonina, post-weaning fast, body condition, circadian rhythms, activity budget, electroencephalogram

Introduction

The transition from maternal provisioning to independent feeding is a critical period for young mammals. During the suckling period, pups rely entirely on maternal milk [1], [2] whereas after weaning, to be able to survive, they must develop the physical and physiological capacities and behavioural skills necessary to independently forage and acquire sufficient resources to cover their overall metabolism [2], [3], [4], [5], [6], [7], [8]. Marine mammals forage at great depths and, as is required for air breathers, surface between dives for oxygen replenishment [9], [10], [11], [12], [13], [14]. Their foraging aptitude depends on dive durations and depths constrained by their oxygen reserves and diving abilities [11], [15], [16], [17], [18], [19], [20], [21].

Different maternal care strategies are observed in pinnipeds [22], [23]. Otariids and Obobenids tend more to be income breeders, with suckling periods ranging from a few months to several years. Mothers alternate foraging trips at sea and shore visits to suckle their pups, thereby allowing prolonged mother-offspring contact [1], [3]. Among phocids, some species such as harbour seals (*Phoca vitulina*) or Weddell seals (*Leptonychotes weddellii*), tend to behave more as capital-income breeders. Their pups are able to swim and dive shortly after birth [6], [10] allowing synchronous dives with the mother during lactation [24], [25]. On the other hand, other phocid species, such as grey (*Halichoerus grypus*), hooded (*Cystophora cristata*) and elephant seals (Mirounga spp.), behave as capital breeders. Females suckle their pups while fasting and mobilizing their reserves accumulated over an extended at-sea foraging trip. After a short lactation period, pups are weaned abruptly and abandoned at the natal site on the shore [3], [4], [22], [26], [27]. Among the latter species, this period is particularly critical as weanlings face the challenge of an amphibious lifestyle: after being born and fed on maternal milk on land or sea ice, the offspring must transition to an aquatic life [1], [3].

After weaning, pups undergo a post-weaning fast (PWF), mainly on land, for several weeks prior to their first departure to sea [28], [29], [30], [31]. The PWF, common to many phocid species [31], is very energy-intensive, with pups losing up to 50% of their lipid reserves and 10% of the protein reserves acquired during the lactation period [28], [32], [33], [34], [35]. Although the function of the PWF period is not clearly understood, it is a critical time for the development of coordination and mobility, particularly in the aquatic environment [30], [36], [37], [38], [39]. A number of recent studies have highlighted the importance of the PWF in the development of diving ability, with a significant increase in both blood and muscle oxygen reserves, the development of cardiovascular control and of the main glycolytic and aerobic enzymes activities [36], [40], [41], [42], [43], [44], [45], [46]. Before their departure to sea, total oxygen stores in grey seals and northern elephant seals reach respectively 67% and 75% of adult total mass-specific oxygen stores [28]. The duration of the PWF could also impact the development of diving capacities [47]. In northern elephant seals, a longer PWF than in southern elephant seals (56 ± 16 versus 37 ± 11 days [29]) could explain the differences in the diving abilities of individuals during their first trip at sea, with northern elephant seals diving earlier, longer and deeper than southern elephant seals [47]. At the same time, maintaining limited movement during this period is probably also important to conserve energy reserves [28]. Within a given species, the PWF duration varies between individuals. What is also noteworthy is that in elephant and harp seals, weanlings in better body condition (i.e. heavier in relation to their size, tending to have more adipose and protein tissue at weaning) stay on shore longer than leaner ones [29], [31], [33], [42], [48]. This plasticity in fasting duration ensures that leaner individuals have sufficient reserves remaining to travel to favourable foraging areas [49]. However, leaving the beach prematurely can also be disadvantageous for the development of diving skills, as the physical and physiological maturity of young phocids is linked to age [36], [41], [42].

Although physiological and body-composition changes during the PWF have been documented, little is known about the early behavioural development of phocids. This area calls for further attention however, since behavioural as well as physiological components are necessary for the acquisition of swimming and diving skills [6]. Only a few studies have investigated animal behaviour during the PWF, but most of them have focused on diving, and the others have only consisted of fixed-hour observation [29], [30], [36], [37], [38], [50]. No previous studies have used biologgers to detail behavioural changes during the PWF in relation to the body condition at weaning.

In this regard, the southern elephant seal (SES hereafter, *Mirounga leonina*) represents a particularly interesting model. It is the largest phocid species whose pups nurse for only about 21 days before undergoing a PWF lasting 5-6 weeks [51]. There are few data on the behaviour of weaned SESs during the post-weaning period on land [29], [30], [38], [50], and any link with the body condition of individuals is unknown. Thanks to its fairly long PWF and its amphibious lifestyle during this period, the SES is an excellent model for studying the post-weaning behavioural development of weanlings in preparation for aquatic life.

The main objective of our present study is to investigate the behavioural changes in weaned SESs during the PWF period according to their body condition at weaning. We hypothesised that active behaviour, particularly swimming and diving, increases with age, and that changes should occur earlier in leaner individuals. Furthermore, we hypothesised that in order to reduce their energy expenditure, pups in poorer body condition tend to be less active than their counterparts.

Material and Methods

All data processing was performed using Python version 3.9.13 [52] on Spyder 5.3.2.

To explore behavioural changes during the post-weaning period, we analysed the activity budgets and movements of weaned female SESs monitored by accelerometery, Argos/GPS and EEG data, on the Kerguelen Islands (49°27'S and 70°54'E).

1. Animals and Instruments

Female pups were captured and sedated following the procedure described elsewhere [55]. For each pup, size (standard length) was measured to the nearest centimetre and body mass was measured to the nearest kilogram.

In December 2014, 10 weaned female SESs (age > 4 weeks post-weaning) were each fitted with a DSA tag (SCOUT-DSA-296, Wildlife Computers) and a SPOT tag (SPOT-293 Wildlife Computers) glued on their head and back fur respectively (Araldite® AW 2101, Ciba, see Supplementary Material, Table S1 for detailed information).

Subsequently, between 2020 and 2022, 20 newly weaned female SESs (19-24 days old) were equipped with accelerometer ± Electroencephalogram (EEG, hereafter) recorders glued on their head fur using fast-setting epoxy glue (Araldite® AW 2101, Ciba), divided as following (see Supplementary Material, Table S2):

- 13 pups with Axytrek® logger (Axytrek® Marine, TechnoSmArt, Italy)
- 4 pups with Axytrek® + EEG recorder (Neurologger®3, Evolocus LLC, USA)
- 3 pups with Neurologger®3 system including only an accelerometer, without EEG recording.

The loggers were recovered 2 to 26 days after deployments (see Supplementary Material, Table S2 for detailed information on tagging numbers, types and durations by individuals).

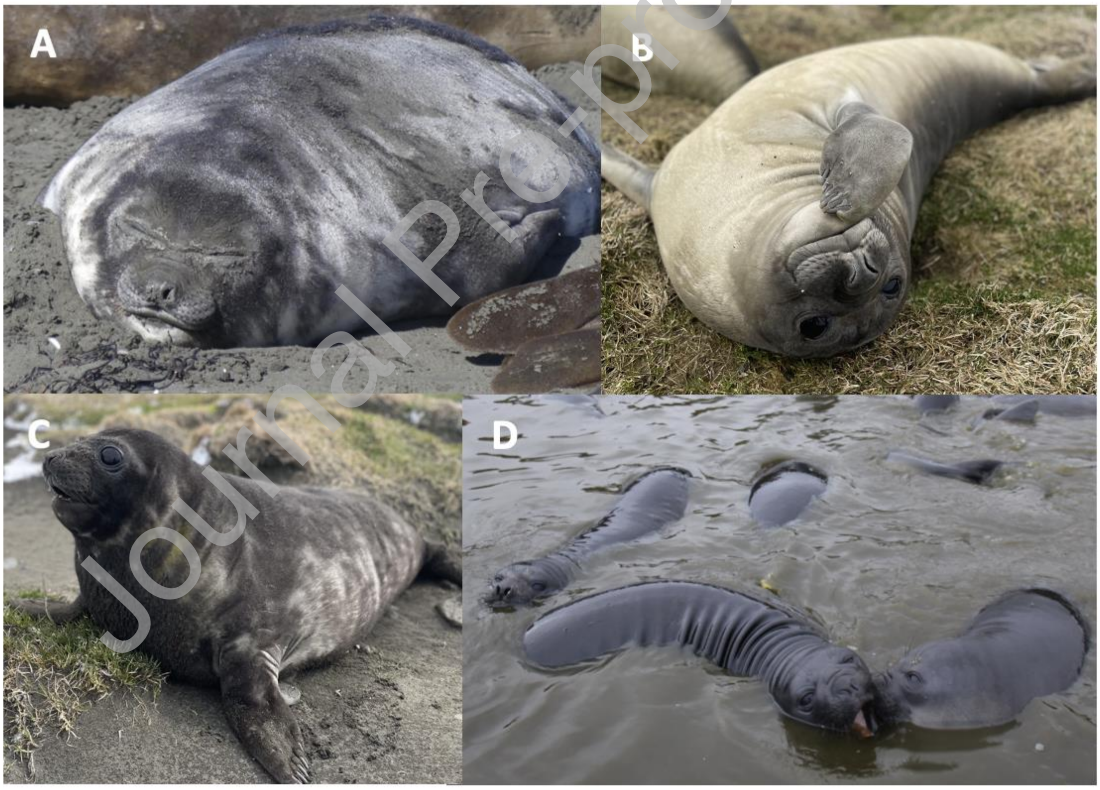
2. Data collection

1.1. Accelerometry and Argos data just prior to their departure to sea

The DSA tags recorded pressure at a rate of 1Hz and were set to start emitting when pressure exceeded 5 meters. Real-time diving data were transmitted via the Argos satellite system (Collect Localisation Satellite-CLS, Toulouse, France) and all tag specifications were described in [53], [54]. The SPOT tags transmitted Argos positions when the animals were at the surface.

1.2. Accelerometry and GPS data just after weaning

In order to obtain body condition data independent from body length, we determined, based on the method described in [52], the body mass index (BMI) of the individuals as the residual values of the linear regression between body mass and body length at weaning. Depending on the logger, acceleration was sampled at ~36Hz (Neurologger®3) or 25 Hz (Axytrek®). Axytrek® also recorded the animal's GPS location every minute (when satellites were detected). In 2021, on 3 pups, the accelerometer recording was associated with a manual scoring of their behaviour every 30 seconds for a period of 90 minutes after they were equipped, and twice a day for 60 minutes until they were



Behaviour	Description
Resting	SES is motionless, eyes are open or closed (A)
Quiet Waking	SES is performing low intensity movements without displacement (scratching, rolling etc) (B)
Moving	SES is moving on ventral surface using fore- and hind-flippers and could play with other pups (C)
Swimming	SES is moving in water performing hind-flipper strokes (D)

Fig. 1 Ethogram of newly weaned female southern elephant seal (SES) behaviour with illustration for each state. A, Resting. B, Quiet Waking. C, Moving. D, Swimming.

unequipped (see Supplementary Material, Table S2). To characterise activities in relation to accelerometer recordings, four major behavioural states were identified (Swimming, Moving on land, Quiet Waking and Resting, see details in Fig. 1), and we removed the 30-s periods during which multiple behavioural states were observed.

1.3. EEG data

Six pairs of sub-cutaneous electrodes for EEG recording (13 mm long and 0.40 mm in diameter, Spes Medica, Italy, ref: MN4013D10S) were fixed to the fur, in frontal, parietal and occipital areas of the right and left hemispheres (see Supplementary Material, Fig.S1 for electrode positions), using fast-setting glue (Loctite Super Glue, Henkel). EEG signals were recorded using a differential amplifier at a sampling rate of 500 Hz. Binary electrophysiological data were converted into European Data Format using a customised MATLAB application (Neurologger Converter & Visualizer ©, Evolocus LLC).

3. Accelerometry-based behaviour classification

Acceleration data were downsampled to 25 Hz for the Neurologgers and used to compute 10 separate variables (4 temporal and 6 frequential features used and described previously [56], [57], [58], [59], [60], see Table 1 for details) measured over 30-s periods. The first 5 minutes and the last 60 minutes of the data were excluded from the analyses to avoid the effects of anaesthesia or handling disturbances. Static and dynamic accelerations were separated and processed according to existing studies [18], [61], [62], [63], [64] to extract the animal's position (pitch and roll) variance, overall dynamic body position (ODBA), and number of hind-flipper movements. All body orientations were corrected before analysis, using pitch and roll at the initial stage, assuming that the animals were perfectly straight at that time. To extract frequential features, a fast-Fourier transform was performed on each axis, and the maximum power spectral density peak was selected with its associated frequency [60], [65], [66].

Table 1. **Summary of predictor variables extracted from acceleration data**

Variable	Description
ODBA	Overall Dynamic Body Acceleration
Pitch, Roll var	Pitch and Roll variance
Hind-flipper strokes	Number of hind-flipper movements corresponding to swimming movements
PSD X, Y, Z	Dominant power spectrum density in each axis

Main Freq. X, Y, Z	Frequency corresponding to the dominant power spectrum density in each axis

The acceleration data from the behaviourally scored animals were extracted and temporally mapped to the 4 behavioural states to create a training dataset as input for our classification algorithm. Following a recent behavioural classification study on phocid seals [60], we applied a random forest algorithm [67] using the "Scikit-Learn" Python library (version 1.0.2) and the "RandomForestClassifier" algorithm. The data were split into 70/30% training and test sets, and a stratified k-fold cross validation method was used to train the algorithm due to class imbalances. Model performances (precision, recall and F1 statistic as described in Shuert et al. [60]) were calculated from the confusion matrices resulting from each cross-validation used with the testing dataset.

4. Accelerometry data processing

Using acceleration data from animals with exactly known weaning dates (n=17, see Supplementary Material, Table S2-S3), behavioural states were predicted over 30-s period data using our classification model. Activity budgets were calculated according to the age since weaning (in weeks) and the time of day. As the recordings were not of the same duration, individuals did not all have the same amount of data. For each behavioural state, the mean was then calculated as a weighted mean based on the amount of data per individual. We computed the average daily activity budget for each week after weaning to investigate temporal changes.

The time-of-day results were stratified into four periods of the day: night (20:00-03:00), dawn (03:00-06:00), day (06:00-17:00), and dusk (17:00-20:00), according to the procedure provided by the US National Oceanic and Atmospheric Administration (https://gml.noaa.gov/grad/solcalc/).

5. GPS and SPOT data processing

SPOT data were filtered to only include Argos data of high quality (i.e. quality 1, 2 or 3) prior to the pups' departure from Kerguelen Island.

To analyse the evolution of the animals' movement over time, daily distance covered was calculated as the sum of the partial distances between each GPS/ Argos point recorded by the loggers on the animals.

6. EEG data processing

For the animals equipped in 2022 with Neurologger®, accelerometry data were classified by our random forest model and only the "Resting" periods were selected for the following analyses. In conformity with the standard described in the American Academy of Sleep Medicine sleep scoring manual [68], electrophysiological signals were band-pass filtered between 0.3-45 Hz to prepare for visual sleep scoring. The signals were visualised at a single epoch time scale of 30-second and a voltage scale of 80 µV. For visual sleep scoring, the guidelines were based on those established in previous marine mammal studies [69], [70], [71], [72]. Based on previous studies in northern elephant seals [70], [73], we scored sleep, in 30-s epochs, according to the following sleep states: Slow-Wave Sleep (SWS), Potential REM (resting + apnoea just after SWS period), Quiet waking (resting + eupnoea, unlikely to be REM) and Active. As electromyograms and electrocardiograms were not recorded and animals were not video tape, REM sleep could not be clearly distinguished from the awake state. Using the z-axis of the gyroscope, we visually detected breaths [70], and scored “Potential REM” as apnoeic resting periods occurring just after SWS period [70], [73].

7. Statistical analysis

Statistical analyses were performed with Python (version 3.9.13) [52], using the “scipy.stats” module (version 1.7.1). To test for differences in movement behaviour and age, daily distances covered were log-transformed on the basis of the data’s assumed normality, and we used a Student’s *t*-test. To test for differences in the mean number of at-sea positions and age, we used a Mann-Whitney U test. To test for differences in the proportion of behaviours in relation to age or body condition, we used a χ-squared test of independence.

Results

BMI ranged from -22 to 32, with a median of 0.05, and two separate groups were clearly identifiable. Individuals with a BMI of less than 0.05 were considered as “Lean” (n=9, mean=-13.5, SD= 8.3) and the others as “Corpulent” (n=8, mean=12.0, SD=10.5) (t_{15}= -5.50, $p<$ 0.05, see Fig. 2A and Supplementary Material, Table S3 and Fig.S2).

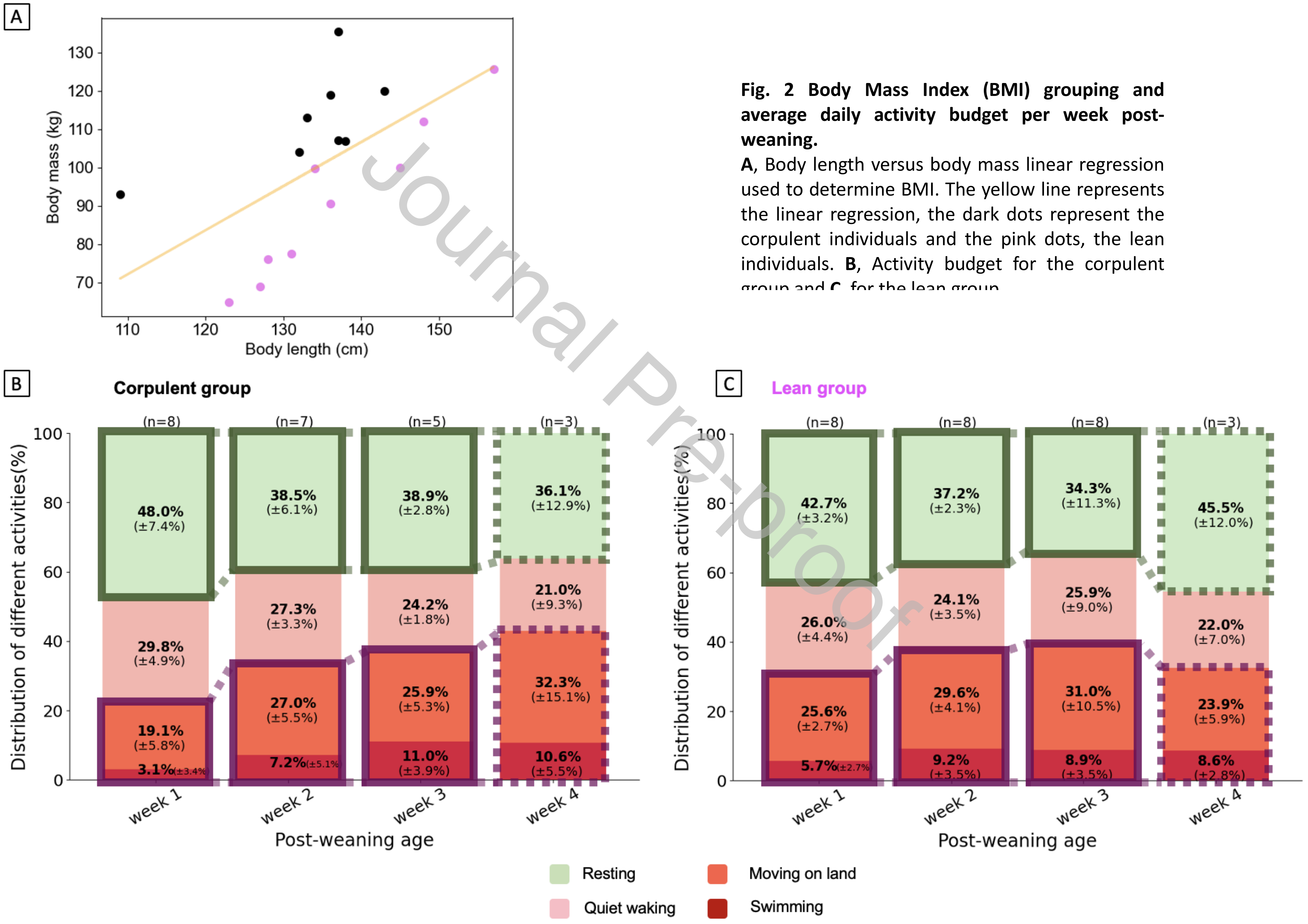


Fig. 2 Body Mass Index (BMI) grouping and average daily activity budget per week post-weaning.
A, Body length versus body mass linear regression used to determine BMI. The yellow line represents the linear regression, the dark dots represent the corpulent individuals and the pink dots, the lean individuals. **B**, Activity budget for the corpulent group and **C**, for the lean group.

1. Movement activity

To understand how the activity of weaned SES pups increases with age just after weaning, we used GPS data, recorded between 2020 and 2022. A total of 16 of the 17 GPS recordings were analysed. The data of one individual were excluded because of GPS recording issues.

The average daily distance travelled by SES pups did not differ according to body condition (t_{43}= 0.80, p=0.43). Thus, the two groups were combined for this analysis. Between the first week and the third- and fourth-weeks post-weaning, the average daily distance travelled increased significantly (Fig. 3A, t_{25}= -2.53, p= 0.019 and t_{18}= -2.12, p= 0.048 respectively). During the first 15 days following weaning, the daily distance covered was not significantly different (t= -0.85, p=0.40), but increased considerably after the third week (Fig. 3A). The weanling elephant seals travelled an average of 1,320 ± 428 m (mean ± SE) per day during the first and second weeks, compared with 2,198 ± 568 m (mean ± SE) during the third week, and 3,050 ± 904 m (mean ± SE) during the fourth week post-weaning. As well as the daily distance covered increasing with age, the area of activity also expanded (Fig. 3B and 3C). Between the first, second and third weeks post-weaning, the mean number of positions recorded at sea increased significantly (Fig. 3B, U= 9, $N_{\text{week 1}}$= 10, $N_{\text{week 2}}$= 6, p= 0.02 and U= 14, $N_{\text{week 1}}$= 10, $N_{\text{week 3}}$= 12, p= 0.002 respectively), as shown on the GPS tracks in Figure 3C. Due to the low quantity of data recorded in week 4 (n=3 for each group), the results for this week simply showed a trend and should be viewed with caution.

Thanks to Argos data recorded with the SPOT tags in 2014, we studied the movements and dispersion of individuals at a later stage, just before their departure to sea. A total of 7 of the 10 Argos recordings were analysed, due to Argos transmission issues for the other 3 individuals.

One week before their departure to sea, the daily distance travelled and the dispersion of individuals were visually greater than during the first 4 weeks post-weaning, as observed in Fig. 3C-D. The weanling elephant seals travelled an average of 5,480 ± 749 m (mean ± SE) per day during their last week ashore. As the locations were far from each other, even separated by bays, this illustrates a substantial time spent in the water, swimming (Fig. 2D).

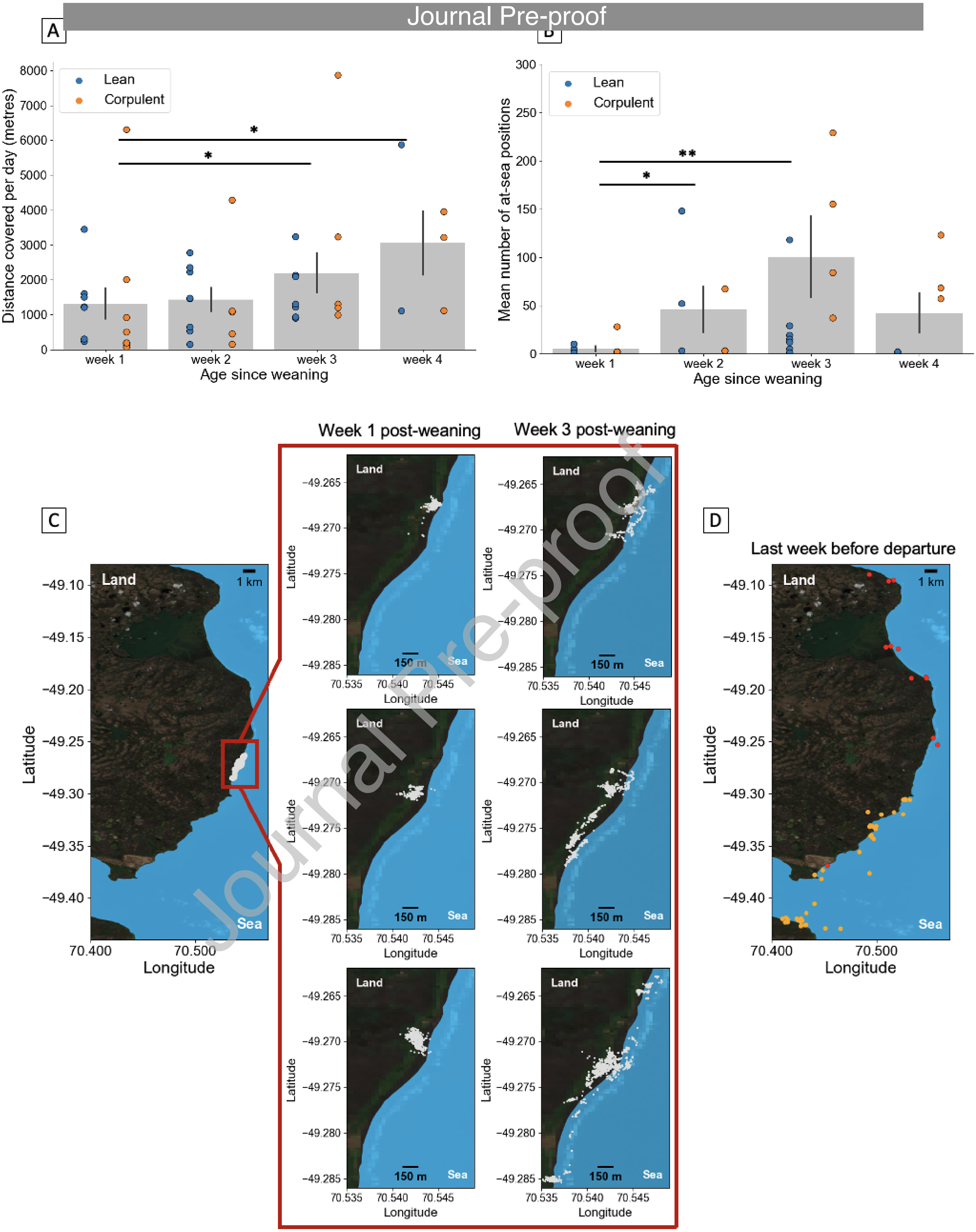


Fig. 3 Movement activity of weanling SES during the PWF.

A, Average daily distance covered (in m) from week 1 to week 4 post-weaning (mean ± SE) and **B**, Mean number of at-sea positions from week 1 to week 4 post-weaning (mean ± SE) for the individuals (n=17) equipped with Axytrek tags between 2020 and 2022. **C**, GPS tracks of 3 pups equipped in 2020 and 2021, 1 and 3 weeks post-weaning. **D**, Argos positions of 2 pups equipped in 2014 (one in red and the other in orange), one week before their departure to sea. *=$p<0.05$ and **=$p<0.01$

2. Average daily activity budget per week post-weaning

To characterise behavioural changes in SES weaned before their first trip to sea, we classified accelerometer data during the post-weaning period of the individuals recorded between 2020 and 2022.

2.1. Random forest accelerometry-based behaviour classifier from accelerometers

Using a random forest model, we could reliably classify four behaviours (Resting, Quiet Waking, Moving, and Swimming, Fig. 1) during the post-weaning in newly weaned SESs (Table 2). The behaviours were consistently well classified in terms of precision (true positive accuracy), recall (sensitivity), and F1 (harmonic mean of Precision and Recall) between training (70%) and testing data (30%) despite the class imbalances (Table 2). “Grooming” and “Moving” were the two least accurately classified behaviours due to classification errors between these two categories (see Supplementary Material, Table S4). However, their results are still acceptable (Table 2).

Table 2. **Random forest classification report on the testing set**. Precision (positive predictive value), Recall (sensitivity), and F1 (harmonic mean of Precision and Recall) for the four behaviours modelled using a random forest algorithm. Values closer to 1 indicate better model performance.

Behaviour	Precision	Recall	F1	Total test observation
Resting	0.98	1.00	0.99	125
Grooming	0.92	0.81	0.86	27
Moving	0.84	0.89	0.86	18
Swimming	1.00	1.00	1.00	5

To identify the most important variables for classification, we used the mean decrease impurity method. Impurity approaches zero as the data become separated. Thus, a larger Mean decrease impurity indicates that the variable is more important for differentiating behaviours within our random forest model. Therefore, of the predictor variables derived to summarise the acceleration data, the dynamic acceleration component (relating to body movements) was found to be the most important in classifying behaviours (see Supplementary Material Fig. S3). The ODBA is the most important variable, followed by the maximum power spectral density for the lateral axis and the pitch variance (see Supplementary Material Fig. S3).

2.2. Description of the average daily activity budget per week post-weaning and before leaving for the first ocean trip

To compute the average daily activity budget, a total of 805,215 30-s periods from 17 individuals were classified with our random forest model. The first 3 weeks following weaning were well recorded (between 198,357 and 296,203 30-s periods per week) while the fourth week was less detailed (55,632 30-s periods) as the individuals had either departed to sea or were too far from the study site and had therefore been unequipped.

2.2.1. *General changes in activity budgets*

The time spent on each activity was affected by age (X^2_9= 1014.17, $p< 0.05$) and by body condition (X^2_3= 135.44, $p< 0.05$, Fig. 2B-C and Supplementary Material Table S5). During the first 3 weeks post-weaning, the time spent resting decreased for both groups, but for a given age, corpulent pups spent more time resting than leaner individuals (Fig. 2B-C and Supplementary Material Table

S5). Conversely, the time spent active (Moving + Swimming) increased with age for both groups, although lean-group weanlings were more active during the first 2 weeks than corpulent individuals, both on land and in water (Fig. 2B-C and Supplementary Material Table S5). After the second week, the situation reversed, with the corpulent individuals spending more time in the water in week 3 (Fig. 2B-C and Supplementary Material Table S5). Due to the low quantity of data recorded in week 4 (n=3 for each group), the results for this week simply showed a trend and should be viewed with caution.

2.2.2. *Activity distribution throughout the day*

To investigate activity patterns during the day, the average daily activity budget was analysed according to the 24-hour day cycle. Both groups exhibit a clear circadian pattern with pups being particularly active at dawn and dusk (Active behaviours > 50% of the time during dawn and dusk), while resting mainly during the day (Resting > 50% of the time and Moving behaviours < 10% of the time between 11am and 5pm, Fig. 4). Quiet Waking behaviour remained relatively stable throughout the day, with a slight drop when activity levels were highest (Fig. 4). This pattern was maintained throughout the whole post-weaning period prior to the pups' departure to sea but with an increasing amount of time spent active, and in particular in the water, at dawn (swimming behaviour > 20% of the time at dawn from the third week post-weaning age, Fig. 4 and Fig. 3C) and dusk.

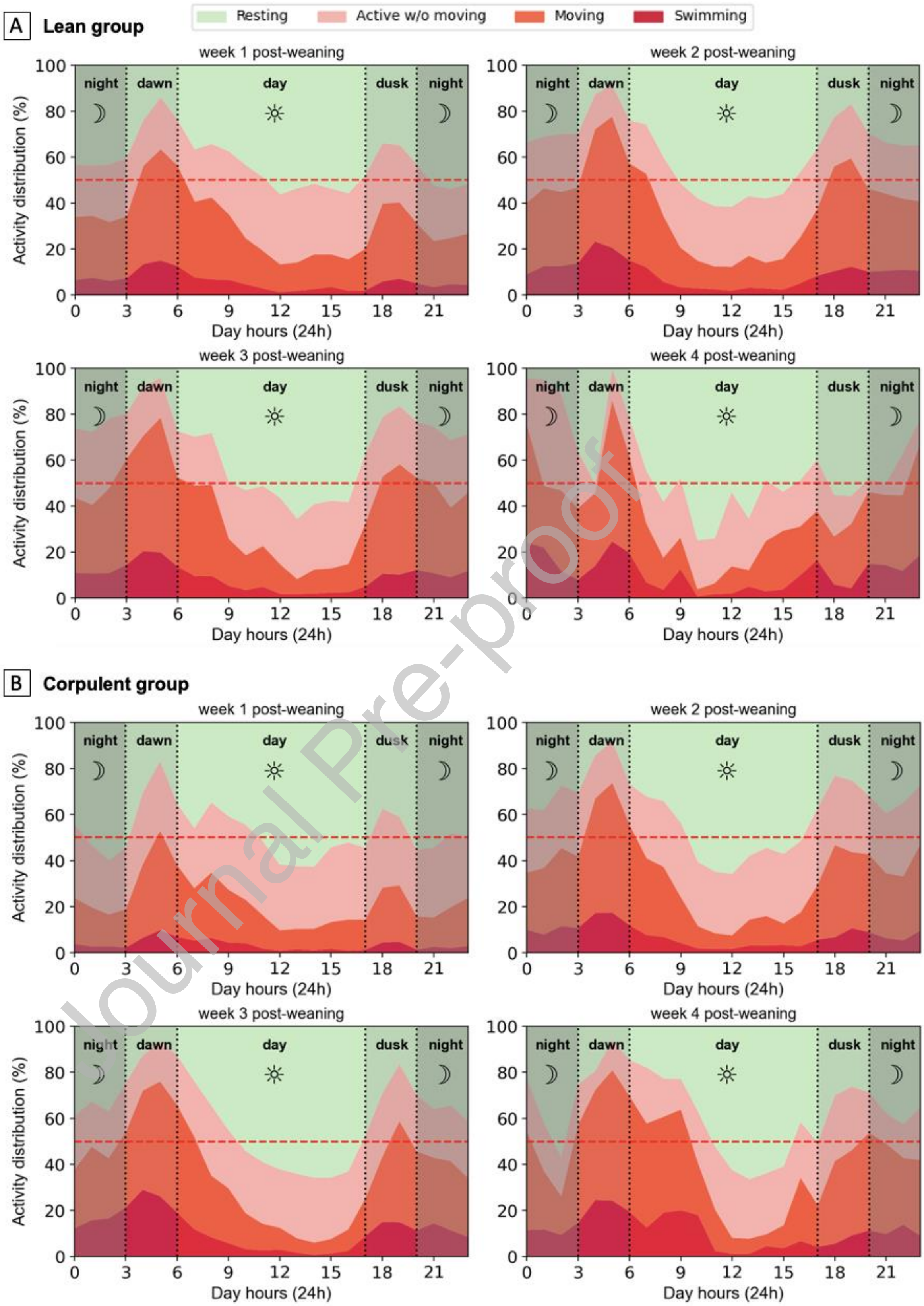


Fig. 4 Distributions of activity budgets according to daytime and age since weaning for A, the lean group and B, the corpulent group (from week 1 to week 4). The stratification of the day into four periods is representing by the black dotted vertical lines. The red dotted horizontal line represents 50% proportion.

3. Description of resting periods

The EEG data from one individual was excluded because the usable recording data lasted less than 24 hours. A total of 3 EEG recordings (223 hours recorded, 120.5 hours usable) were analysed to visually score the "resting" periods and extract the SWS periods from “Potential REM” and “Quiet waking” periods (Fig 5A). Two recordings were performed during the first post-weaning week (indiv Ids 553 and 559) and one during the second week (indiv Ids 605). Time spent in SWS accounted for between 34% and 40% of daily “resting” time, and “Potential REM” for between 5% and 9% of daily “resting” time. Out of all behaviours considered over the day, the individuals spent between 3.9 and 5.5 hours per day in SWS and, between 0.5 and 1.2h per day in potential REM (Fig. 5B).

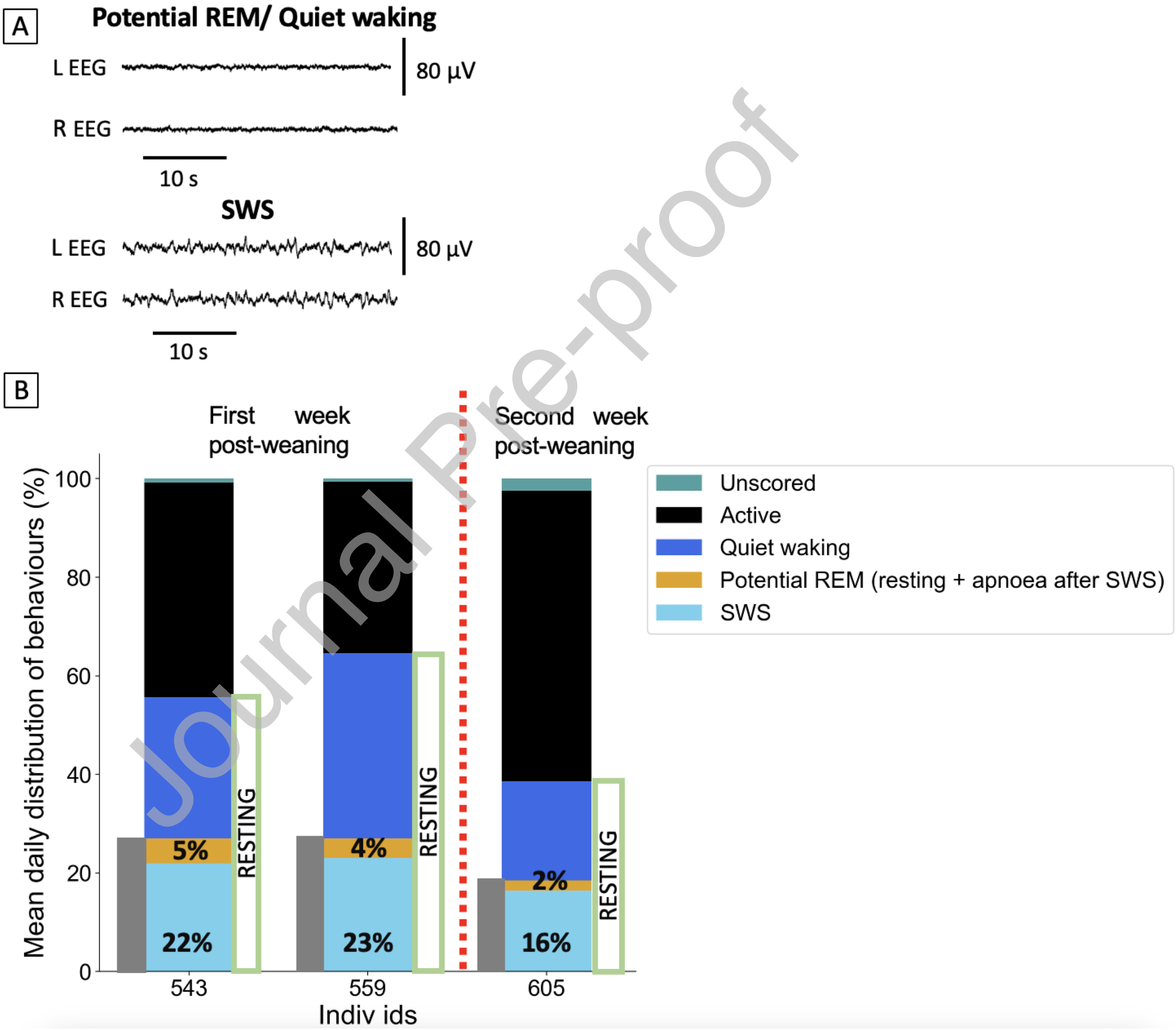


Fig. 5 Sleep patterns during the first two post-weaning weeks (n=3 EEG recordings). **A**, 30-s EEG period showing a distinction between SWS (high-voltage and low-frequency waves) and Potential REM or Quiet waking (low-voltage and high-frequency waves) stages. **B**, Mean daily SWS quotas for SESs during the first and the second post-weaning week.

4. Diving behaviour just prior to the first at-sea foraging trip

DSA-tag data revealed that pups on Kerguelen rarely dove before their first trip to sea. One of the 10 tags deployed, set to start emitting when pressure exceeded 5 metres, was never activated before the pup's departure, indicating that this individual never dove up till this point. The others started emitting a few days before pup departure (mean ± SD = 8 ± 4 days before departure). These individuals only performed an average of 12 ± 8 dives (mean ± SD, min. = 2 and max = 26 dives) at about 27 ± 3 m (mean ± SD, min. = 19 m and max = 31 m) for 6.3 ± 0.9 min. (mean ± SD, min. = 4.9 min. and max = 7.7 min.) before departing for their first foraging trip.

Discussion

The post-weaning period is a critical stage for weaned pinnipeds [3], essential for their physiological development [28], [30], [33], [36], [40], [42], [43], [74]. However, only a few studies have focused on physical maturation in preparation for future aquatic life and diving during this 4-5-week period [29], [30], [36], [37], [38], [50]. In addition, to date, no research at all has focused the impact of body condition at weaning on physical development during this period. To fill in this gap, our study directly quantified the behavioural changes of weanlings, according to their body condition, to understand how SESs prepare for their departure to sea, i.e. the transition from terrestrial to aquatic life.

Our population of weanlings was not of homogeneous body size. Thus, we were unable to use weight alone to compare body condition. For this reason, the two groups of individuals were defined according to their individual BMI, based on the study of Orgerets et al. [53]. The calculated BMI, independent of body length, was used to compare the body condition of individuals at weaning [53], [75], and led to clear identification of a group of lean individuals and a group of corpulent ones.

We applied a supervised-classification method to three-axis accelerometer data to monitor the behaviour of weaned SESs. In previous studies evaluating numerous machine-learning algorithms, random forests have been demonstrated as successfully predicting behaviour via accelerometry [76], [77]. This algorithm has thus been widely implemented to classify the behaviour of a large range of animals (e.g. [78], [79], [80]), including pinnipeds [60], [77], using temporal and frequency predictor variables. In our study, this model produced good results on both the training and test data, although our training set was not very large and its different categories were unbalanced. As suggested by Ladds et al. [77], our training and testing sets included several individuals of different body sizes to obtain a more robust model for predicting the behaviour of many weaned SES. The four behavioural categories selected for this analysis (Resting, Active w/o moving, Moving and Swimming) were representative of the behaviour of weanlings in the wild [30], [37], [38]. Resting had the least cases of misclassification, as it had minimal movements on all axes and was therefore easy to classify, as shown by other studies [60], [77]. Active w/o moving and Moving were predicted with the least accuracy in training and testing steps, the two being most often confused, which is not surprising given that the behaviours overlap and our datasets are limited. Although the Swimming category was only defined via visual scoring in small ponds and the sample size was very limited, this behaviour was very well classified. This result may be explained partly because this behaviour produces an accelerometer signal that is distinct from the other behaviours, in particular the presence of fin strokes. Despite the sound performance of our model, it is uncertain whether it could be used for other age categories.

The use of accelerometers to monitor behaviour on land, combined with a supervised-classification method, provided an overview of the pups' activity budget during the PWF. We showed that resting was the most common behaviour of weanlings during daylight hours and that activity, both on land and at sea, increased at night, particularly at dawn and dusk. These behavioural descriptions are similar in other elephant seal populations and some phocid species, with particularly long rest periods around midday [6], [30], [31], [37], [38], [81], [82], [83]. Harbour seals and Weddell seals exhibit the same rhythm, with less time spent in the water during the afternoon [6], [83]. This circadian pattern becomes more prominent as the animals grow older [30], [38]. In older northern elephant seals, it has been suggested that night-time activity may reduce predation risk [84]. Although our data suggest twilight activity peaks, we cannot link them to predation avoidance as no predation has ever been reported on the Kerguelen shoreline by killer whales or sharks. Instead, this tendency can be linked to the fact that adult elephant seals forage more efficiently at dawn and dusk when their prey perform nychthemeral migration, and then at night rather than during the day when prey are located deeper and are therefore less accessible [85].

We hypothesise that the more intense activity observed at dawn and dusk reflects an internal cycle. Whether this circadian rhythm is endogenous or triggered by maternal or congener activity during suckling remains to be demonstrated. In other phocid species, such as the bearded seal, this circadian rhythm can be modulated by tidal rhythm [38], [86], or shifted toward daylight. Unlike the phocids mentioned above, which tend to be more nocturnal, bearded seals tend to be diurnal [87], [88]. Variations in foraging depths, benthic versus pelagic foraging, and diets between species, could explain this difference, with relatively shallow benthic foragers being more light-dependent than deep-foraging species such as Weddell or elephant seals.

In the activity budgets, “Resting” behaviour data were insufficient to differentiate sleep from wakefulness. The use of EEG refined the pups’ activity budgets during the PWF, distinguishing SWS and “Potential REM” periods. However, without electromyograms, electrocardiograms and associated video, we were unable to obtain a complete sleep scoring including REM periods with absolute certainty [68], [70], [71]. According to the individuals, the daily quota of SWS periods ranged from 3.9 to 5.5 hours during the first two post-weaning weeks. Unfortunately, due to the movement behaviour of weanlings, we were unable to perform EEG recordings on older individuals. The values obtained for the younger weanlings are slightly more than half those recorded on land in 2- and 4-month-old northern elephant seals and the REM quota is also reduced in SESs [71], [73]. Different experimental conditions, different physiological stages, and the short recording duration, did not allow a reliable comparison between these two age categories. However, environmental and ecological processes, such as habitat conditions or physiological constraints, may be involved to explain these differences between northern elephant seals and SESs. In SESs, a shorter maternal dependency and PWF period compared to northern elephant seals [29] forces them to hasten their physiological maturation and possibly incompletely before their first at sea-departure [47], which may lead to shorter sleep periods. In addition, tougher weather conditions and the presence of numerous peripheric male with fights may affect sleeping periods. Studies on harp seals have revealed that daily SWS amounts decrease during the first month of the animals' lives, just after weaning. The same trend could be observed in SESs due to behavioural changes during this period. Weanlings are more active than juveniles and adults, which could explain the lower SWS values. Performing additional recordings of pre-weaning pups and of 2-month-old pups would provide new information on the evolution of sleep quantity during the post-weaning period in SESs.

During the post-weaning period, the pups must maintain a low energy expenditure to survive the fast while preparing for their first trip to sea [33], [49]. However, as they age and lose mass, weanlings’ movements increase regardless if they are lean or corpulent. The same behaviour has been observed on Marion Island and Valdes Peninsula, although the distances travelled are different

[29], [38]. On Marion Island, SESs rarely travelled far from their natal beach [29] whereas on the Kerguelen Islands and in Argentina they can disperse up to 50 km from their birth area [38], [50]. The configuration of the coastline (small isolated bays versus long stretch of beaches) as well as predation risk could explain these behavioural differences [29], illustrating the behavioural adaptation of weaned SESs to their environment [3]. This increase in distance travelled suggests an improvement in swimming skills. While young weanlings drift passively in shallow waters due to wind-driven surface currents, older individuals deliberately move along the coast as their swimming/apnoea capacities improve [36], increasing their dispersion [50]. The distance travelled per day by weanling SESs increases with age, but the movement pattern is similar between lean and corpulent pups. Admittedly, our GPS data must be considered with caution. Indeed, if the logger detected no satellites, it switched to standby mode for 20-30 minutes before trying to take a new position. In addition, submersion of the logger, the position of an individual leaning on its back on the shore, or a cloudy sky could reduce satellite visibility, leading to a drop in the number of positions recorded during such episodes [89]. Although the trend in our results was relevant, absolute values were rather coarse.

As in grey seals, maintaining limited movement is probably advantageous for both groups to conserve energy reserves [28]. This suggests that differences in physical development between lean and corpulent weanlings are not related to movement patterns but more likely to the time allocated to resting or active behaviours. We expected that leaner pups would have a lower level of activity as a mean to reduce their metabolisms and therefore preserve their body store. However, we found the opposite. Although resting is the most common behaviour, clear differences in the activity budgets between lean and corpulent weanling SESs emerged. Leaner pups were more active earlier than corpulent ones, both on land and at sea, and spent less time resting. However, as they aged, the opposite trend was observed. These behavioural changes are likely to be related to differences in body store between the two groups and could possibly lead to ecophysiological differences. In marine mammals, usable oxygen stores are preferentially found in their red blood cells and muscles [90], [91], [92], and compared with terrestrial mammals, their blood volumes, haematocrit, haemoglobin and myoglobin contents are very high [93], [94], [95], [96], [97]. Previous studies have also highlighted that although marine mammals have high body O_2 stores, their pups are physiologically immature and must develop these stores during growth [1], [6], [10], [21], [42], [44], [46], [98], [99], [100], [101], [102]. It has been shown that oxygen storage capacity in the muscles develops very quickly after weaning and is not improved by a longer period on land in phocids [40], [42]. However, these studies did not consider behaviour.

Significantly, more active behaviours associated with muscular hypoxia favour myoglobin synthesis [103], [104], [105]. The myoglobin stock of lean pups could thus be boosted and the development of their muscle oxygen storage accelerated compared to their more corpulent congeners. As lean pups are more constrained by their lower body store, it is critical for them to depart to sea as early as possible and in any case before the full depletion of their store. Therefore, developing their oxygen stores as fast as possible might be critical to allow an early departure to sea. In support of this hypothesis, a previous study has shown that the development of blood oxygen stores is faster in lean pups compared to corpulent ones [40]. In this way, benefiting from an earlier and faster synthesis of myoglobin due to their early active behaviour, lean weanlings can rapidly increase their apnoea and therefore increase their dive duration. Interestingly, contrary to our predictions, both Axytrek and DSA-tag data revealed that pups on Kerguelen rarely dove and never deeper than a few meters prior to departing for their first at-sea foraging trip. One of the DSA tags, set to start emitting when pressure exceeded 5 meters, never transmitted prior to pup departure to sea while the others only recorded around ten shallow dives, performed only a few days before the pups' departures. Also worth noting is that on the first day of their departure from shore for their first at-sea foraging trip, the mean diving depth of 10 female pups equipped with DSA tags was 44 ± 29 m, max. 94 m, with a mean duration of 5.1 ± 1.1 min., max. = 8.5 min. (mean ± SD, unpublished data). These observations suggest that through the PWF, apnoea aptitudes develop more than absolute diving depths.

In phocids, as in grey or elephant seals, this development would compensate for the shorter PWF of lean individuals [28], [31], [49], enabling them to depart to sea with sufficient oxygen reserves to dive and forage. However, a longer PWF improves cardiovascular control [106] and the ability to suppress oxygen consumption during breathing [74]. Pups are faced with a trade-off between staying ashore for a long time to improve their diving physiology but reducing their fat reserves, or leaving earlier with greater energy reserves but poorer physiological capacities [31], [47]. This would explain the differences in diving behaviour between individuals during their first trip to sea [47], [107]. In northern elephant seals, a longer offspring dependency and PWF duration allow weanlings to develop diving behaviour much faster than SESs and to reach deeper and longer dives earlier in their first year at sea [47]. Therefore, future studies should investigate the relationship between the development of oxygen stores and the activity of pups during the PWF. Secondary factors such as habitat, predation and diet may also influence the ontogeny of diving behaviour [47].

These behavioural and physiological changes during the post-weaning period enable weaned SESs to prepare for their first trip to sea, which lasts several months. In addition to the development of physical aptitude and oxygen stores, we can also expect them to undergo brain maturation. In mammals, brain maturation in neonates is associated with a decrease in resting periods [108], [109], [110], [111]. However, the proportion of time dedicated to true sleep during those resting periods remains unknown. Assuming that drift dives represent sleeping dives, elephant seal females spend only 2 hours per day sleeping while at sea [71]. It would thus be worth monitoring how the deep sleep / resting pattern of pups changes over the PWF. Sleep in adult elephant seals is currently being studied on land and at sea relying on dive characteristics ground-truthed by EEG [71]. Applying this method to weaned SESs during the post-weaning period would provide a more detailed understanding of ontogenic changes in activity within this species. Adaptation to aquatic life then evolves gradually throughout the first foraging trip at sea, with diving duration and depths increasing over time [53].

Ethics

The "Comité d'Ethique ComEth Anses/ENVA/UPEC" validated all scientific procedures performed on elephant seals under the project (no APAFiS: #32407-2021071212163407 v2): Physiological and energy expenditure adaptations of elephant seals to environmental constraints during their life cycle as part of the IPEV programme 1201-CycleEleph. All animals in this study were handled and cared for in total accordance with its guidelines and recommendations.

Data, codes and materials

The datasets supporting the conclusions of this article and all scripts used for data treatment and analysis are available upon request.

Supplementary figures and tables are provided in electronic supplementary material.

Author's contribution

C. GUINET, C. GILBERT and J. BADAUT conceived the ideas and obtained funding; E. PIOT, L. HIPPAUF, L. CHARLANNE collected the data; E. PIOT designed the model and E. PIOT with B. PICARD performed the data and statistical analysis; C. GUINET, C. GILBERT, and J. BADAUT supervised data analysis; all authors participated in the discussion and interpretation of results; E. PIOT, C. GUINET, C. GILBERT and J. BADAUT led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Competing interests

We declare we have no competing interests.

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