

Foraging behaviour of tuna feeding on small schooling *Vinciguerria nimbaria* in the surface layer of the equatorial Atlantic Ocean

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Abstract

The feeding behaviour of small tuna on the mesopelagic fish *Vinciguerria nimbaria* was studied in an equatorial area of the Atlantic Ocean (10–20° W, 0–5° N). Acoustic data (from a scientific cruise) and tuna stomach content data (from the tuna purse-seine fishery) were combined. *V. nimbaria* formed loose schools that occurred in clusters during daytime, and large aggregations during the night. The characteristics of the schools and clusters were analysed. The average length, size and packing density of the day-school were estimated at 48.5 m, 24 400 individuals, and 5.8 fish m⁻³, respectively. The average length of clusters was close to 10 km. The packing density of night-school was estimated at 1.6 fish m⁻³. The preying of tuna on *V. nimbaria* was modelled as a stochastic process based on two Poisson processes. Daily rations of tuna were estimated at 3.5% and 7% of the body weight. Taking into account the swimming performance of the prey and the predator, we showed that tuna were able to feed on day-schools in a very short time, whereas feeding during the night by filtering was not competitive. Furthermore, a cluster is able to feed a single tuna school during 2 months, proving the sustainability of the biomass of small tuna in the area by *V. nimbaria*.

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1. Introduction

Fish develop a broad variety of feeding strategies (Lazaro, 1987; Gerking, 1994). Two main feeding behaviours are observed among pelagic species: particulate feeding (including fish that eat other fish) and filter feeding. The former is distinguished from the latter by the visual detection of prey. Both types of feeding may be sequenced in successive events. Faced with prey that form schools, the predation-act can be split into two phases: seeking out the school, and then catching prey inside the school. The first phase includes detection and pursuit, the second, capture by sight or filtration, according to the packing density of the school, the reaction of the prey, the illumination and the retention ability (mouth and branchial filters).

Tropical tuna grow rapidly and have high swimming performance. They live in the pelagic ocean environment which has been generally considered as poor in prey (Blackburn,

1968). They can shift from one food source to another, preying upon anything they encounter (if they can capture and ingest it). They thus feed on varied prey including numerous fish, crustaceans, squid and gelatinous organisms. They do not always chase individual prey but commonly seek out schools of favoured targets (Gerking, 1994). To feed on fast swimming epi-pelagic fish, like sardines or anchovies that form highly dense schools on the continental shelves, tuna have to track and eat them as quickly as possible. Faced with small prey that form loose schools and swim slowly, tuna have to adapt their capture strategy. Are tuna able to use some kind of filtration? Indeed, most species of tuna have well developed gill rakers (Magnuson and Heitz, 1971). If the tuna feed during the night, such an apparatus could prevent food loss through the operculum gap.

In an equatorial area of the Atlantic Ocean (10–20° W, 0–5° N), where large purse-seine fishery occurs, the presence of seasonal tuna concentrations was studied within the context of a research programme, PICOLO, conducted by Institut de Recherche pour le Développement (IRD) (Ménard et al., 2000a). In this area, skipjack (*Katsuwonus pelamis*) and

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juveniles of yellowfin (*Thunnus albacares*) and bigeye tuna (*Thunnus obesus*) of the same size (average fork length 46 cm) feed mainly on small-size mesopelagic fish *Vinciguerria nimbaria* (Phosichthyidae) (Ménard et al., 2000b). This foraging fish aggregates day and night in the top 200 m of the sea (Marchal and Lebourges, 1996). In this context, the feeding behaviour of the tuna and the predator-prey relationships were studied based on acoustic data and tuna stomach content data. Concentrations of *V. nimbaria* were observed during the scientific sea cruise P1 that took place in January-February 1997. This survey was conducted onboard the IRD R/V “Antea” in the area extending from 5° N to 0°. North south transects along the longitude 15° W was replicated eight times. The aim was to estimate the size of the schools, the distances between the schools and the packing densities of the schools. We also looked at the number of *V. nimbaria* in a dataset of tuna stomach content. We estimated the average meal size and the daily consumption using a mixed Poisson-Poisson model for a predator preying on a homogeneous prey (Magnússon and Aspelund, 1997). Taking into account the swimming performance of the prey and the predator, we then investigated the feeding behaviour of tuna during the day vs. the night, and the sustainability of the biomass of small tuna in the area by *V. nimbaria*.

2. Materials and methods

2.1. Acoustics

The R/V “Antea” was equipped with a dual-frequency (120 and 38 kHz) hull-fixed transducer echo sounder (OS-SIAN, trademark). Continuous records were made during the entirety cruise. For this study, only the 38 kHz frequency was used. The packing density inside the aggregations, the size and the dimension of the schools, as well as the distance between schools have been acoustically assessed in relation to the time of the day and the depth, using the software Movies+ (Diner et al., 1989; Weil et al., 1993). Acoustic settings are displayed in Appendix A. Data is processed by layer (average Sv) and by school in the depth range 10–200 m. Movies+ provides many characteristics of each school, as physical or acoustics properties (Scalabrin and Massé, 1993). The data was corrected for geometry and density descriptors (Diner, 1999). When the correction was seemed improbable after the algorithm was applied, the school was discarded. We also applied a statistical correction to convert the average observed length of the school into “true” diameter by a factor of $4/\pi$, assuming a circular horizontal section (MacLennan and Simmonds, 1992). Packing densities were computed from Sv values, using a target strength (TS) of -56.7 dB for a 43 mm standard length (SL) and 0.6 g wet weight *V. nimbaria* (Lebourges-Dhaussy et al., 2000). A backscatter threshold for schools was defined as a minimum packing density (Swartzman and Hunt, 2000). We used 1 fish m^{-3} for night time and 2 fish m^{-3} for daytime, i.e. -56.7 and -53.7 dB, respectively. An efficient recursive function of

S+SpatialStats (Kaluzny et al., 1998) was used to find the nearest neighbour distances between the day-schools. Frequency distributions of the variables characterising the schools are highly asymmetrical, and maximum values are outliers. In our approach, the population mean is the characteristic of interest. We used a robust procedure from a library of S-PLUS 6 to fit lognormal distributions and to estimate the lognormal means and the standard errors. There is several ways to define a cluster of schools. Petitgas et al. (2001) used a distance threshold. Here, cluster size was investigated using two independent methods with two datasets: the number of recorded schools per kilometre and the integration by depth layer per kilometre (i.e. the area backscattering strength averaged per kilometre; MacLennan et al., 2002), assuming that all the detected biomass was in schools. The first dataset we collected was smoothed with a moving average of order 1: a cluster was encountered when the number of schools per kilometre was greater than the mean in the smoothed series. In the second approach, the cluster size was estimated by the range of the variogram of the integration by depth layer per kilometre. This second method seems confident because it takes into account the intensity of the detection, the depth range in which the day-schools occurred, and avoid the use of a threshold. A spherical function was chosen to model the empirical variogram.

2.2. Micronekton observation and sampling

Observations included trawl sampling with a young-fish mid-water trawl (mouth of 10 m high and 15 m wide, 10 mm mesh in the cod-end), equipped with a trawl echo sounder. Trawling was targeted on school groups or scattering layers detected by echo sounding. Hauls ranged from depths of 20–135 m, with an averaged duration of 30 min. SLs of *V. nimbaria* specimens were measured and some fish were weighed (wet) at the laboratory.

2.3. Stomach content analysis

Stomachs were collected on tuna caught during daylight hours by the purse-seine fishery operating in the area. The length of each sampled fish was measured and the stomach was preserved in formalin or was deep-frozen. Stomach contents were weighed (wet) and sorted according to the food item and the degree of digestion. Four degrees of digestion similar to those used by Magnuson (1969) were assigned to each item, according to the state of the ingested prey. The rate of empty stomachs was very high, but a substantial number of small size tuna had only *V. nimbaria* as prey (for more details, see Ménard et al., 2000b). For these stomachs, *V. nimbaria* were counted and measured (empty stomachs were not taken into account). When identification was not possible, an empirical method based on the degrees of digestion was used for reconstructing the initial prey-weight prior to the digestion (Bard, 2001). In this approach, a “test animal” is selected (*Brama orcini* for the ingested fish) in order to compute weight loss factors of prey for each digestion

index. These coefficients allowed us to estimate the initial weight of the stomach content before it was digested. The reconstructed weight was divided by the average weight of an adult of *V. nimbaria* (0.6 g) in order to estimate the number of *V. nimbaria* in the stomach.

Based on the stochastic model of Magnússon and Aspelund (1997), the feeding of tuna that prey on schooling *V. nimbaria* can be described by two random variables. Let X be the number of encounters with prey per unit time interval (i.e. meal frequency), and Y be the amount of food obtained in each encounter (i.e. meal size). The former variable gives the number of schools encountered per unit interval, and the latter the number of prey captured in each encounter with a school. Let T be the length of time a *V. nimbaria* is identifiable in the stomach of a tuna, the amount of food obtained in this interval is

$$Z = \sum_{i=1}^X Y_i$$

assuming that the number of prey consumed in a time interval of length T is the same as the number found in the stomach, and that Y_i is the number of *V. nimbaria* obtained in the i th encounter. A common assumption for foraging models is that both X and Y have Poisson distributions with parameter λ and μ , respectively. Observed frequency distribution of stomach content allows us to estimate both parameters using the method of moments: $\mu = s^2/\bar{z} - 1$, and $\lambda = \bar{z}/\mu$, where \bar{z} and s^2 are the calculated mean and variance of the number of prey in the stomach, respectively. Several assumptions of independence have to be stated. This simple model gives estimates of the average number of meals per unit of time ($\hat{\lambda}$) and the average meal size ($\hat{\mu}$) for small size tuna. These estimates allow us to compute the mean (\hat{C}_w) and variance ($s_{C_w}^2$) of the total consumption (wet weight) in the time interval T :

$$\hat{C}_w = \hat{\lambda}\hat{\mu}\hat{\mu}_w, \text{ and } s_{C_w}^2 = \hat{\lambda}(\hat{\mu}\hat{\sigma}_w^2 + \hat{\mu}\hat{\mu}_w^2) + \hat{\lambda}\hat{\mu}^2\hat{\mu}_w^2$$

with $\hat{\mu}_w = 0.6$ and $\hat{\sigma}_w = 0.21$ g, the average and the standard deviation of the weight of *V. nimbaria* in the area, respectively. If an estimate of T is available, the mean daily consumption can also be estimated (for more details, see Magnússon and Aspelund, 1997). Olson and Boggs (1986) gave values of T from gastric evacuation experiments on yellowfin tuna. T was estimated at 10 h using a mixed group of prey. However, for the small prey *Stolephorus purpureus* (nehu) similar to *V. nimbaria*, T was estimated at 5 h. We thus took these two limits to compute estimates of the total daily consumption by weight and per unit of body weight of a tuna.

3. Results

3.1. Schools during daytime

During the daytime, *V. nimbaria* were schooling (Fig. 1a). The usual depth is around 100 m. We assumed that the schools are circular in horizontal cross-section. The results

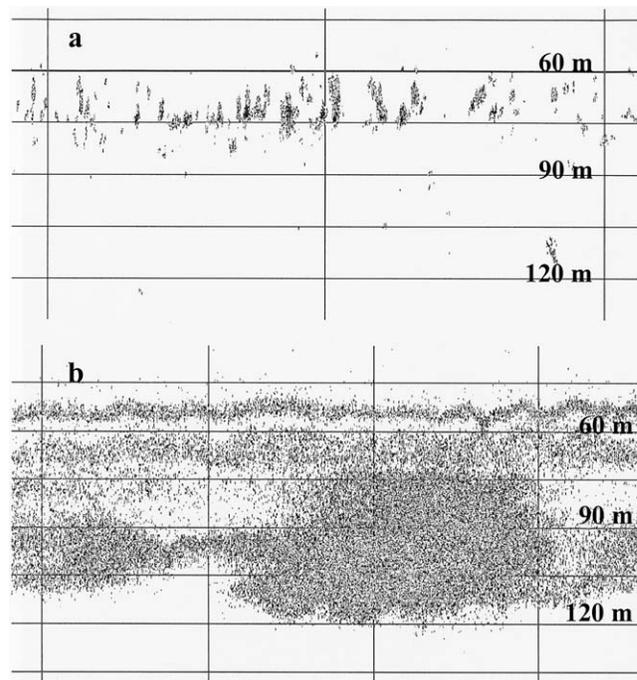


Fig. 1. Echogram showing (a) schools of *Vinciguerria nimbaria* adults during daytime, and (b) one “swarm” during the night. The distance between each vertical line is 1 nautical mile.

on the size of the schools are displayed in Fig. 2. The lognormal mean of the observed length was estimated at 38.1 m (standard error = 0.8). The mean diameter of the schools was 48.5 m after correction by a factor of $(4/\pi)$. The lognormal mean of the height was estimated at 8.3 m (standard error = 0.2). The packing densities of the day-schools were highly variable but rather low given their small size and weak weight (0.6 g in average). The lognormal mean was estimated at 5.8 m^{-3} (standard error = 0.1). The number of fish in a school was then deduced, assuming a school in the shape of a cylinder. The observed cross-section was assumed to be equal to the section of an equivalent cylinder whose height was unknown. The volume of the school was computed from the estimate of the lognormal mean of the section (110.5 m^2), and from the mean diameter of the schools (48.5 m). In average, the number of fish in a school of *V. nimbaria* was thus estimated at 24 400 individuals.

The distances between the day-schools were computed from the relative coordinates in the horizontal cross-section and the depth of the centres of gravity of each of the schools. We selected the schools identified between 50 and 110 m only, because (i) schools were the most abundant in this range, (ii) we limited the bias linked to the acoustic records (variability of the scattering volumes), (iii) and small size tuna can dive to feed at this depth. The lognormal mean of the nearest distance between neighbouring schools was estimated at 124 m (standard error = 5). This is thus a robust estimate of the nearest distance between the gravity centres of the day-schools inside a cluster of schools.

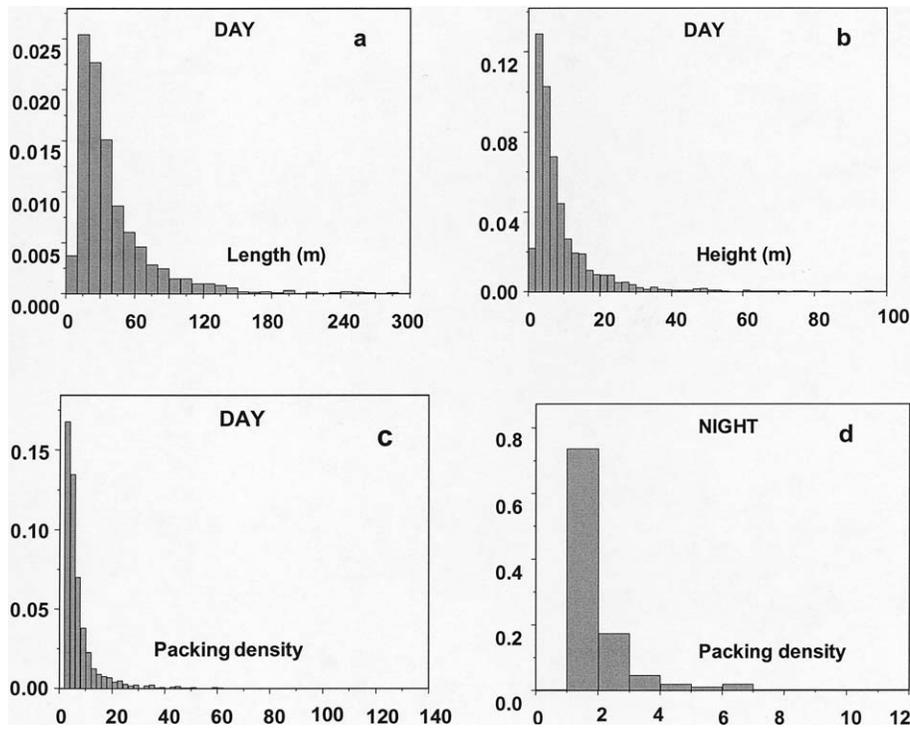


Fig. 2. Histograms scaled as probability densities for (a) the length and (b) the height of the day-schools of *Vinciguerria nimbaria*, and for the packing densities during (c) the day and (d) the night. Robust estimates of lognormal means (standard errors) were 38.08 m (0.77), 8.29 m (0.20), 5.78 fish m⁻³ (0.09), and 1.61 fish m⁻³ (0.06), respectively.

3.2. Clustering

Schools of *V. nimbaria* occurred in clusters during daytime. The total average number of schools per kilometre is 5.5. This threshold allowed us to estimate the average size of a cluster (12.6 km), the average distance between the clusters (11.3 km), and the average number of schools per kilometre inside a cluster (9.7 schools km⁻¹). The empirical variogram for the area backscattering strengths averaged per kilometre shows a plateau (Fig. 3). The range of the corresponding spherical model was estimated at 10.4 km that was very close to the preceding estimation of the size of a cluster. The distance between clusters was highly variable. The clusters

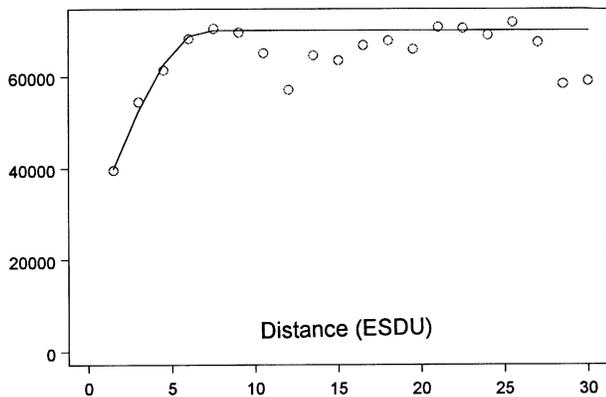


Fig. 3. Empirical variogram and fit of a spherical model for the integration by depth layer and per kilometre (range = 7, sill = 44 000, nugget = 26 000). X-axis is expressed in ESDU and can be converted into kilometre by a factor of 1.482.

probably occurred in groups of clusters. But the acoustical observations recorded during the cruise did not allow us to precisely estimate this spatial organisation. However, the frequency distribution of the distances between clusters showed two patterns (Fig. 4): the main one at short distance (2–19 km), and the other at large distance (41, 61 and 90 km).

3.3. Schools during the night

During the night, *V. nimbaria* were also schooling. Schools were localised at the bottom of the thermocline (80–100 m) or just below (110–130 m). The shape and the size of the schools were completely different from those observed during daytime (Fig. 1b). The sizes we observed were very large, around 3000 m, sometimes twice that. Since the software Movies+ is not adapted to such length of schools, these lengths were directly read on the echograms. The packing density was very low: the lognormal mean is

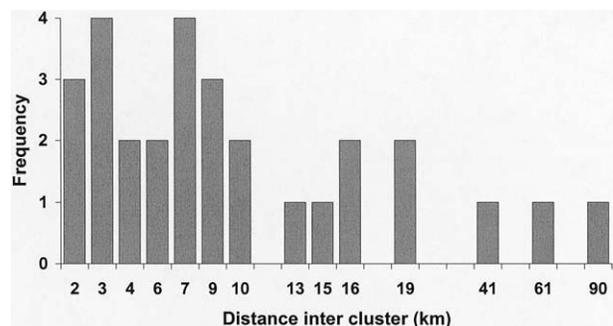


Fig. 4. Frequency distribution of the distances between clusters.

estimated at 1.6 fish m^{-3} , with a standard error of 0.1 (Fig. 2d). The average distance between these schools was about two times their length. They were also grouped in clusters, with very variable but sometimes long distances between them (20 km in average). In reference to krill, we named this type of school “swarm”.

3.4. *Vinciguerria* sampling

The adults of *V. nimbaria* (SL ≥ 30 mm) sampled during the day and the night had the same length distribution (Fig. 5). The juveniles were caught in the surface layer during the night only. These juveniles were not mixed with the adults, instead they were dispersed in layers at the thermocline level.

3.5. Tuna stomach contents

Nearly all of the *V. nimbaria* found in the stomachs of the sampled tuna were adults: they fell into a narrow size range, 39–48 cm. Fig. 6 displays the observed frequency distribution of *V. nimbaria* numbers in the tuna stomachs. The sample mean was 45.4 (variance = 1149; maximum = 150). The average meal frequency based on the Poisson-Poisson

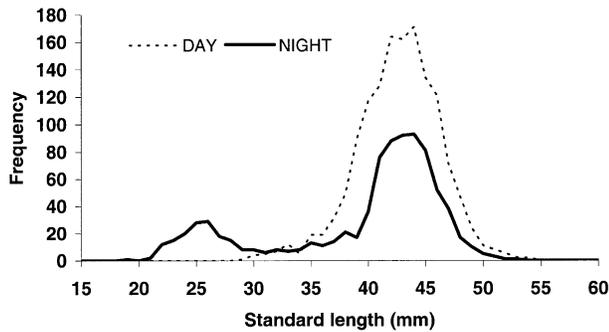


Fig. 5. Frequency distribution of *Vinciguerria nimbaria* standard length, caught night and day by trawling.

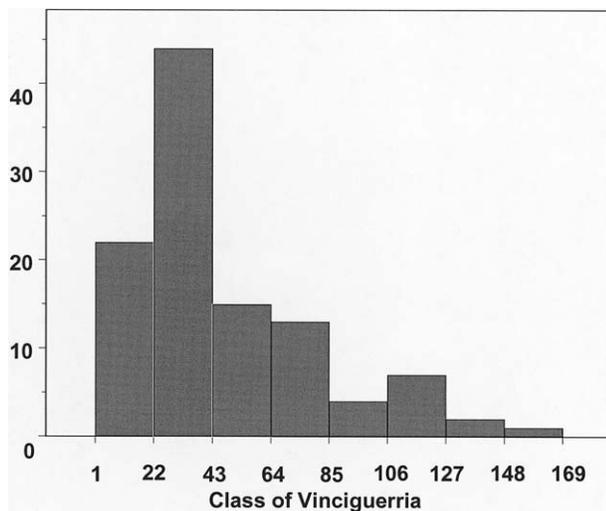


Fig. 6. Frequency distribution of *Vinciguerria nimbaria* number in stomachs of the sampled tuna.

Table 1

Estimates of average number of meals per unit time (λ), meal size (μ), and average time between meals ($1/\lambda$) using the method of moments

Parameter	λ	μ	$1/\lambda$
Estimates	1.9	24.3	0.53

Table 2

Average daily consumption and average daily consumption per unit of body weight as a function of T , the length of time a *V. nimbaria* is recognisable in the tuna stomach

T (h)	Time between meals (h)	Daily consumption (g d^{-1})	Daily ration (per body weight)
5	2 h 50 min	133	7%
10	5 h 40 min	66.5	3.5%

model was estimated at 1.9 meals per unit interval (T), i.e. the time a *V. nimbaria* is recognisable in the stomach, and the average meal size of almost 25 individuals (Table 1). The average and standard deviation of consumption in time T were estimated at 27.7 and 20.9 g, respectively. A tuna with a fork length of 46 cm has an average weight of 1.9 kg. Using the two limits of T (5 and 10 h) based on the gastric evacuation experiments on yellowfin tuna, estimates of the daily consumption and consumption as a percentage of body weight were computed (Table 2). For T equals to 5 h, the daily ration is estimated at 7% of the tuna body weight and at 3.5% for T equals to 10 h.

3.6. Feeding behaviours

The acoustical results and the stomach data are now combined to analyse the foraging behaviour of tuna feeding on *V. nimbaria* schools. Let us consider one single tuna which encounters a cluster of *V. nimbaria* schools during daytime. The feeding involves successive captures of prey with a feeding speed that we ranged from 0.5 to 6 tuna body lengths per second (BL s^{-1}). Equally, we considered that *V. nimbaria* cannot avoid an attack of a tuna predator, because of its small size (no predator avoidance reaction was assumed for the prey). We assumed that the tuna that has encountered a school in the cluster, simply swam at the same depth and at a regular speed, feeding on all the prey he met in front of him. The size of the meal for the tuna was established at 100 *V. nimbaria*. This is a very conservative hypothesis regarding our estimations ($\hat{\mu} = 25$), but it represents roughly 3.1% of the body weight of the predator. An average packing density of 6 fish m^{-3} leads to an average distance between fish inside the school of $1/\sqrt[3]{6} = 0.55 \text{ m}$. According to its speed, the tuna filled its stomach in less than 15 min (Fig. 7a). At 6 BL s^{-1} , the computed time to catch 100 preys was only 2 min. Now, let us consider the same tuna encountering a swarm of *V. nimbaria* during the night. Since visual detection of prey is not possible, the tuna is assumed to feed by filtration. In this theoretical case, the time to prey on the same number of *V. nimbaria* depends on the packing density, the gap of the mouth and the speed of the fish. The mouth section was assumed to be circular and the radius was estimated at

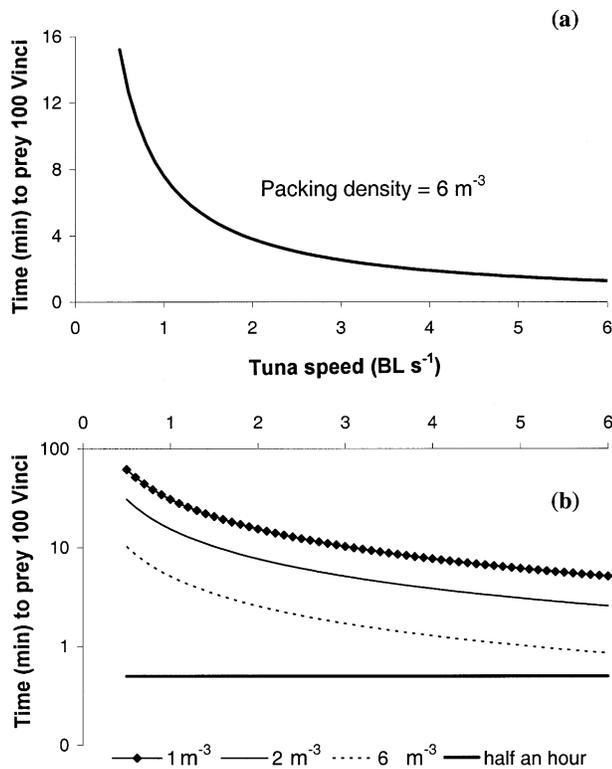


Fig. 7. Computed time for one tuna to fill its stomach with 100 *Vinciguerria nimbaria* as a function of tuna speed and packing density. (a) Model for the day; (b) model for the night.

0.025 m (unpublished data). We supposed that the tuna swam with its mouth open. The time necessary to fill its stomach was calculated as a function of the packing density (varying from 1, 2 and 6 fish m⁻³) and of the tuna velocity (Fig. 7b). At 2 BL s⁻¹, the tuna needed between 3 and more than 15 h to fill its stomach, depending on the increasing values of the packing density.

Now let us consider a school of small tuna (mean individual weight = 1.9 kg). Such a school, which weighs 38 metric tons on average (purse seine catch statistics in the area), has 20 000 individuals. Based on the estimated daily rations (mean of 7% and 3.5%), 3 million *V. nimbaria* have to be fed on by tuna each day (prey biomass = 1.8 metric tons), corresponding to 126 day-schools. Assuming that a cluster of schools is isotropic, considering the number of schools per kilometre inside the cluster, and the average diameter of a cluster, the number of schools inside a cluster is estimated at 8000. Thus, a cluster is able to feed a single tuna school during 2 months, or 63 schools of tuna during 1 d.

4. Discussion

The estimate of the packing density is dependent on the TS of *V. nimbaria*. TS measurements of mesopelagic fish are scarce. Bagøien et al. (2001) measured the TS of adults of two mesopelagic fish, *Maurollicus muelleri* and *Benthoosema glaciale* (−59.3 and −58.0 dB, respectively), using a split-beam 38 kHz. Both species are close in shape and size to

V. nimbaria. According to their data, we computed the average SL of their samples: 42.9 and 55.5 mm, respectively. Thus, for the same size, the difference is 2.6 dB between *M. muelleri* and *V. nimbaria*. Measurements were made in the near-surface waters during the diel vertical migration, following the same procedure we followed for *V. nimbaria*. Bias could affect both measurements, especially if the fish was swimming up during the experiment (Torgersen and Kaartvedt, 2001). It is thus difficult to interpret this difference that could be related to the species. For example, the swimbladder of *V. nimbaria* is well developed, probably more than the other species (Marshall, 1960). Anyway, even a bias of ±3 dB (that doubles or divides by 2 our packing density estimates) could not modify the conclusions with respect to the tuna feeding pattern. The packing density we estimated looks very low in comparison with those of true pelagic fish. However, such low densities were also recorded with other mesopelagic fish in “dense” layers. In the Gulf of Oman, trawling by the R.V. *Dr. Fridtjof Nansen* equipped with a krill trawl led to a catch of 0.6–1.6 fish m⁻³ during the night, and 8 fish m⁻³ during the day, of *Benthoosema pterotum*, a very common small Myctophid (Sætersdal et al., 1999).

The thresholds and the acoustical parameter setting are also key parameters. Moreover, the day-schools of *V. nimbaria* appear to be very loose, and the night-swarms very large. In order to compare day and night data, we set the same signal thresholds for both aggregations, but we made different choices for schools and layer. Indeed, the −59 dB acoustical value used for schools also catches other scatters during the night. The −50 dB threshold discards most of them and reduces slightly the integrated day-values in comparison with the −59 dB threshold (about 10% less). But in this study, the integration layer process was only used for characterisation of the clusters, and not strictly for biomass estimation. However, the relation between the night-swarms and the clusters should be more investigated.

The preying of tuna on *V. nimbaria* is modelled as a stochastic process based on two Poisson processes. No satiation effect are taken into account, and the underlying hypotheses of independence are sometimes hard to hold, i.e. the time between meals is independent of the size of the meal, schools are assumed to be randomly distributed. This simple approach can be extended using, for instance, a Poisson-negative binomial model, as proposed by Magnússon and Aspelund (1997). However, the aim here was to have simple estimates of meal size and of daily consumption of tuna feeding on schooling *V. nimbaria*, using stomach content data that were not sampled at the same time as the acoustic data. We thus did not take into account the empty stomachs and other prey than *V. nimbaria* was ignored. Especially, the time spent by one tuna to seek a cluster of prey schools has not been assessed. But the time for one tuna to join one school to another inside a cluster is negligible, because of the short average distance between them. Therefore, our daily consumption results concern tuna who found schools of

V. nimbaria. If empty stomachs would had been included in the analysis (but no representing sample was available), the overall encounter rate and the consumption estimates would have been lower. But our results in terms of daily rations (between 3.5% and 7%) were similar to those obtained elsewhere. Using a completely different approach based on stomach contents, Olson and Boggs (1986) estimated the ration of yellowfin tuna of the Eastern Tropical Pacific Ocean at 3.9% of the fish's body weight. Ménard et al. (2000b) followed the same procedure and found that the daily ration varies from 1% to 6%. Furthermore, Magnuson (1969) quoted that the maximum capacity of the stomach of a captive skipjack tuna was about 7% of its body weight.

Tuna clearly do not always hunt individual prey but seek out schools of favoured targets. Once a concentration is detected (the encounter with a group of prey), the feeding involves successive captures of individuals, given a handling time and a "feeding" swimming speed for tuna that in this case fed on a quasi-static prey. Actually, skipjack tuna is one of the scombrids species with the fastest recorded cruising speeds. But the sustained speed in scombrids is variable, ranging from 1 to 10 BL s⁻¹, whereas burst speeds can reach 12–15 BL s⁻¹ (Altringham and Shadwick, 2001). On the other hand, the small size of *V. nimbaria* leads to a swimming speed of one order of magnitude less than the swimming speed of tuna. Measurements were made with a split-beam on a similar species (Torgersen and Kaartvedt, 2001). These authors found an average speed of about 30 cm s⁻¹. We thus considered that *V. nimbaria* cannot avoid an attack from a tuna predator. Furthermore, this mesopelagic species is probably not adapted to support a high level of light. The length of time tuna feed on *V. nimbaria* during daytime remains very short. We did not take into account the handling time, and we certainly slightly underestimated the total feeding time. But the computed time for feeding during the night is probably higher. Actually, the speed of a tracked skipjack tuna was recorded in the area. This tuna swam in a cluster of schools during daytime (Fig. 11 in Marchal et al, 1996). Its average speed was about 2 BL s⁻¹ and its track was linear in direction and depth. During the night, the same fish was swimming more slowly. Thus, small surface tuna are able to feed during daytime on very loose schools of small fish in a very short time. On the opposite, feeding during the night by filtering is definitely not competitive in this context, and may explain why tuna do not use this type of feeding.

Schooling behaviour is common among fish, but the characteristic pattern of schooling behaviour is variable (see Fréon and Misund, 1999). For epi-pelagic fish (e.g. anchovy), the schools are generally large and their overall packing density is very high in comparison with *V. nimbaria*. However, *V. nimbaria* compensate by a high number of small day-schools grouped in clusters in the surface layer, whereas such a fish normally lives at depth during daytime. In that sense, *V. nimbaria* is a favourable target-prey for small size tuna in the equatorial Atlantic Ocean. The underlying simple assumptions we used to study the foraging behaviour of tuna

feeding on schooling *V. nimbaria* allow us to make more qualitative, rather than quantitative, conclusions. Simple feeding models based on information on school density and distances, swimming speed and detection range of the predator, combined with independent assessment of encounter rate estimated from stomach analysis, seem a promising tool for investigating foraging behaviour.

Appendix A

A.1. Acoustic settings

Acquisition threshold = -65 dB.

A.2. Processing settings

Parameters	Day	Night
(1) Schools		
Minimum signal threshold (dB)	-59	-59
Maximum signal threshold (dB)	-10	-10
Minimum school Sv threshold (dB)	-53.7	-56.7
Minimum length (m)	10	500
Maximum length (m)	5000	5000
Minimum height (m)	2	20
Maximum height (m)	100	100
Minimum area (m ²)	20	500
Maximum area (m ²)	100 000	100 000
Authorized horizontal gap (ping)	2	0
Authorized vertical gap (m)	2	0
Minimum depth processed (m)	20	80
Maximum depth processed (m)	200	200
Processing distance (nautical mile)	2	10
(2) Layers		
Minimum depth processed (m)	10	10
Maximum depth processed (m)	200	200
Total number of layers	10	10
Processing distance (nautical mile)	1	1
Minimum signal threshold (dB)	-50	-50
Maximum signal threshold (dB)	-10	-10
(3) Target strength (dB)		
<i>Vinciguerria nimbaria</i> 43 mm SL	-56.7	-56.7

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