Does tuna school size depend on fish size?

L. Dagorn [1], M. Petit[1], J-P. Hallier[2], P. Cayré[3] and M. Simier[4]

Abstract:

The aim of this study is to examine French purse seiner data in the Indian Ocean from 1984 to 1991 in order to study the relationship between the tuna size and the tuna school size. Purse seiners were chosen because catches can be considered as schools. Only free schools are studied. School sizes are evaluated in number of individuals which compose the school. Non-parametric statistics are computed to test if, for each fish weight class, the number of individuals in the schools varies. The results show that there are significant differences between classes, so we can consider that tuna school size depends on fish size. While the fish size is increasing, the school size is decreasing. Some assumptions are advanced to explain this tendency. It appears that for yellowfin tuna, we could link the evolution of the school size to access to new types of preys. The changes in hunting methods or the ideal free distribution model helps us to understand these results, but we need more precise studies before being able to explain the exact relationship between the fish size and the school size.

Résumé:

L'article a pour but d'étudier les relations entre la taille des thons et la taille de leurs bancs. Les données utilisées proviennent des pêches des senneurs français dans l'océan Indien de1984 à 1991. La pêche à la senne permet de considérer que la prise correspond au banc entier. Seules les captures sur mattes libres ont été retenues. Les tailles des bancs ont été évaluées en nombre d'individus. Des méthodes statistiques non-paramétriques ont permis de tester si la taille des bancs diffère selon la classe de taille des poissons. Les résultats montrent qu'il y a des différences significatives entre les diverses classes. On peut donc considérer que la taille des bancs est en partie reliée à la taille des thons qui les composent: la taille du banc diminue quand la taille des poissons augmente. Certaines hypothèses sont avancées pour expliquer cette tendance. En ce qui concerne l'albacore, il semblerait que l'on puisse relier cette évolution de la taille des bancs avec l'accès des poissons à un nouveau type de proies. Des changements dans la technique de chasse ou encore le modèle de distribution libre idéale nous aident à expliquer ces résultats. Mais il est nécessaire de réaliser dorénavant de nouvelles études plus précises pour mieux comprendre les relations qui lient la taille des bancs à la taille des individus.

Introduction

Fish schooling remains a mystery for man since it is always surprising to see many individuals behaving like a single organism, developing apparently difficult group organization. In his review on the functions of schooling behavior in teleosts, Pitcher (1986) says that << predators and food are the keys to understand fish shoals >>. There is a continuous evaluation of the benefits and the costs between joining or leaving a group. Much work has been done on the mechanisms developed by schooling fish to counter predators. But, as Partridge *et al* (1983) exposed, few articles have dealt with the functions of predatory fish schools. We have to note the doubt raised by a few authors at the beginning of the 80's about the understanding of tuna schooling. Sharp (1981) wondered << what is a tuna school ? >>, proposing the life of simple size-similar units, with larger schools leading to increased variability of size-related properties. For this author, these simple units could probably be formed by siblings. Cayré (1981) asked if tuna schools are really stable entities with their own individual characteristics or simply temporary aggregations of fish that come together for various reasons. If it is now common to think as Bayliff (1988) that tuna schools do not have a fixed size during all their life, we do not know the parameters which are responsible of the variability in school size. Observing the French purse seiners data in the Indian Ocean (Figures 1, 3), we notice that catches (in tonnes) increase with the weight of individual fish. But as these two variables - school tonnage and fish weight - follow the same tendency, we can wonder if this increased tonnage with the fish weight can be linked to an increased number of individuals in the school or not. From this remark, the aim of this study is to see if the fish weight can act upon the school size. In other words, does tuna school size depend on fish size ?

Materials and methods

We used French purse seiners data in the Indian ocean, from 1984 to 1991. As a first assumption, we propose to consider that the catch from a purse seine set represents the whole school.

We only used catches on free schools and rejected all catches that were made with Fish Aggregating Devices or other floating objects. We consider that such catches are linked with the complex phenomenon of aggregating by floating objects. Our aim is to study free schools that represent the pure schooling behavior. In this work, the species studied are yellowfin tuna *(Thunnus albacares)*, albacore tuna *(Thunnus alalunga)*, bigeye tuna *(Thunnus obesus)* and skipjack tuna *(Katsuwonus pelamis)*. These species are gathered in two groups: (i) yellowfin tuna/albacore tuna/bigeye tuna; (ii) skipjack tuna.

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[1] ORSTOM,
B. P. 172, 97492, Sainte Clotilde Cedex,
La Réunion (FRANCE-DOM)

[2] ORSTOM CRODT/ISRA,
B. P. 2241, Dakar,
SENEGAL

[3] ORSTOM,
213 rue La Fayette,
7501 0, Paris CEDEX 1 0
FRANCE

[4] ORSTOM,
B. P. 5045, 911 avenue d'Agropolis,
34032 Montpellier CEDEX 1,
FRANCE

For each catch, we know the species, the fish weight class and the tonnage of the school. There are various fish weight classes. For yellowfin/albacore/bigeye, we take the following classes (the weights are in kg): < 3, 3 - 10, 10 - 30, 30 - 50, > 50. For skipjack, the classes are: < 1.8, 1.8 - 4, 4 - 6, 6 - 8, > 8.

To compare school sizes for various fish sizes, we must consider numbers of individuals in the schools rather than tonnages. For each fish weight class, we take the middle of the class and we divide the tonnage by this value. In this way, we have an estimation of the number of individuals of the school. We do not show the results that were obtained when we take the minimum or the maximum of each weight class because they were similar. Classes of numbers of individuals are determined: (i) by 100 individuals for yellowfin/albacore/bigeye, (ii) by 500 individuals for skipjack.

For each species, we consider five independent samples, the individual size classes, and we want to test if the populations from which they are coming are different. These samples obviously come from non normal distributions, with many small schools and some extremely high values (Figures 1, 3). Because parametric tests like analysis of variance, need assumptions about distribution parameters (here normality of populations), we choose non-parametric methods also called distribution-free methods. These tests allow comparison of location parameters between samples coming from any unspecified population (Sprent, 1993).

We show results from the MEDIAN test, with the H0 hypothesis: "All the samples come from populations which have the same medians" against the H1 alternative: "Not all medians are equal", without specifying which populations differ in location, how many differences there are.

We also use the WILCOXON rank-sum test for two independent samples, extended to three or more samples by KRUSKAL & WALLIS. It is an overall test for equality of the population means or medians, with otherwise identical and continuous distributions. For *p* random samples, it makes a joint ranking of all the observations from the smallest to the largest. Then, the sums of ranks associated to each sample are computed and compared.

Results

With the selection described above, we have 3,363 schools of yellowfin/albacore/bigeye and 3,026 schools of skipjack.

Each sample is represented by a boxplot. The box extends from the lower quartile (25% of the observations) to the upper one (75%). The length of the box, or IQR for InterQuartile Range, depicts the spread of the middle 50% of the observations. The location of median is shown by the horizontal line inside the box, the mean by the star. The whisker lines extend from the quartiles to the adjacent values (most extreme values inside 1,5*IQR, beyond the upper and lower quartiles). The white and black circles respectively show the outside and the farout extreme values. Group medians are connected by a dashed line. The width of each box is proportional to the square root of the number of observations in that group. This representation: (i) shows the shape of the distribution for each sample (we can notice asymmetry and presence of outliers); (ii) allows visual comparisons between samples.

At first, for the yellowfin/albacore/bigeye grouping, we notice an increase of the tonnage with fish size and a decrease of the number of individuals (Figures 1, 2). For skipjack, we notice the same increase for the tonnage, except for fish over 8 kg (Figures 3, 4). We observe a slow decrease of the number of individuals. The non-parametric tests will now be used to test the difference between samples medians, first overall, and then multiple comparisons on every pair of samples.

Yellowfin/albacore/bigeye schools

For the tonnage, the overall tests indicate that the medians are different. The H0 hypothesis (the medians are equal) cannot be rejected when comparing categories < 3 kg / 3-10 kg and 30-50 kg / > 50 kg (Table 1). For the other comparisons, when referring to the median values, we can say that schools of the first class (< 1.8 kg) have tonnages inferior to schools of fish of the last three classes (fish of more than 10 kg). Schools of fish between 3 and 10 kg also have tonnages inferior to the schools of fish of more than 10 kg. Fish between 10 and 30 kg form schools with tonnages inferior to the tonnages of the schools formed by fish over 30 kg.

For the number of individuals, at least one of the medians is different. All the tests are significant, except the comparison between the classes 10-30 kg and 30-50 kg (Table 2). However, including the previous results about the tonnages, we cannot conclude for the comparisons between the classes < 3 kg / 3-10 kg and 30-50 kg / > 50 kg. The numbers of individuals are different but not the tonnages, so the difference can only be due to the calculation of the numbers of individuals.

To summarize, for yellowfin/albacore/bigeye, numbers of individuals of schools decrease from the class of fish inferior to 3 kg to the classes of fish over 10 kg, for the class 3-10 kg to the same classes (over 10 kg) and for the class of fish between 10 and 30 kg to the class of fish over 50 kg. It seems that the weights 10 kg and 50 kg are thresholds in the evolution of school sizes by fish weights.

Skipjack schools

For the tonnage, the results of the overall test show that the medians are different. But the H0 hypothesis (the medians are equal) cannot be rejected when comparing categories 1.8-4 kg / 6-8 kg, 1.8-4 kg / > 8 kg, 4-6 kg / 6-8 kg 4-6 kg / > 8 kg and 6-8 kg / >8 kg. For the other comparisons, when referring to the median values, we can say that the schools formed by fish of weight inferior to 1.8 kg have tonnages inferior to the schools of the other classes. The schools of the class 1.8-4 kg have tonnages inferior to the schools of class 4-6 kg.

For the numbers of individuals, the overall test gives the indication that at least one of the medians is different. Considering the previous results about the tonnages, we do not examine the comparisons between the following classes: 1.8-4 kg / 6-8 kg, 1.8-4 kg / > 8 kg, 4-6 kg /6-8 kg, 4-6 kg / > 8 kg and 6-8 kg/ >8 kg because the differences can be due to the calculation of the numbers of individuals. For the other categories, we can conclude that schools of class < 1.8 kg are smaller than schools of class 4-6 kg and schools of class > 8 kg. Schools of class 1.8-4 kg are smaller than schools of class 4-6 kg.

To summarize, for skipjack, we can keep in mind that the numbers of individuals in schools decrease when we pass from class < 1.8 kg to class 4-6 kg, from class 1.8-4 kg to class 6-8 kg. For the largest fish, we can only say that schools composed of fish over 8 kg have less individuals than schools composed of small fish (< 1.8 kg).

Discussion

From troll-catches and purse seiner data, Roger (in press) distinguishes two different feeding strategies: (i) tuna form small schools in poor areas, feeding on what they meet; (ii) tuna form large schools feeding on large concentrations of prey-fish. Following the author, our purse seiner data represent tuna in large schools feeding on rich areas. Our results show that tuna school size depends on fish size. While the school tonnage increases with fish size, the school size (in number of individuals) seems to decrease.

We only found two authors dealing with the relationships between the fish size and the school size. Sharp (1981), citing Breder (1965), evokes the << loosening >> of bluefin tuna schools *(Thunnus thynnus)* with increased size. He comments these results saying that it is not atypical of large tuna like yellowfin. Inversely, Pitcher (1986) explains experiments made by Pitcher *et al.* (1983), showing that larger fish tend to be in larger schools. But these observations were made on fish-prey: minnows (*Phoxinus phoxinus*) and dace (*Leuciscus leuciscus*). So, with this author, we can assume that the size does not have the same effect on school size depending on the nature of the fish (prey or predator). Our results are in the same way of the remarks of Sharp (1981).

Robinson and Pitcher (1989) demonstrate that cohesiveness of pelagic schools varies inversely according to hunger. They predict that << fish with similar levels of hunger and recent feeding history should be found in descrete shoals >>. Roger (in press) reached the same conclusion when he said that we find small tuna schools in poor areas and larger schools in richer areas. Petit (1991) proposed a mathematical model defining the tuna school size from the richness of the waters, or the inverse, the richness of the waters from the school size. The increased prospected volume is balanced by the sharing of resources, controlling the school size. But, if the variability of school size seems to be explained by the richness of the areas, how can we interpret the variability of school size in relation to fish size on rich areas ?

We can note that it seems to have a threshold in this decreasing tendency. With the yellowfin results, the previous analysis shows that for fish under 10 kg, the schools tend to be large, while over 10 kg, they tend to be smaller. This threshold approximatively corresponds to the value of 83 cm found by Roger (1990). Below this size, the maximum prey size and the mean prey size are increasing with the predator size. Over 83 cm, tuna seem to be able to eat every prey-size. Our assumption is that this access to a new class of preys is responsible for the school size decreasing. Micronektonic epipelagic fish which are the preys of surface tuna are fast swimmers. Although large tuna can eat smaller preys, they seem to prefer to concentrate their attacks on large preys when they are present in the search area. But, when the preys are swimming faster, the predators are spending more energy to catch them. The costs/benefit ratio would be in favour of the predator, since it prefers eating such preys. This energy success can be attributed to the high energy gain from these << new >> preys, but also to new techniques developed by tuna in order to decrease energy costs during the hunt. Partridge *et al* (1983) studied the structure of 141 schools of giant bluefin tuna *(Thunnus thinnus)*. The internal structure of these schools (from 2 to 79 individuals) supports two hypotheses for the formation of predatory fish schools. <<The parabolic shape of the schools suggests that tuna hunt cooperatively and the position of fish within the schools is such that individuals benefit from hydrodynamical interactions with their neighbors >>. The cooperative hunt and the hydrodynamic advantages represent tools for energy conservation. Partridge *et al* (1983) precises that, in the parabolic shape, no simple rule of positioning could be followed by all individuals. We can assume that this apparently difficult shape is more easily made with small numbers of individuals than with a large number, which can explain the small size of giant bluefin tuna schools. Our purse seiner tuna are smaller than these giant bluefin tuna and the schools are larger, but the principle could be the same. In particular, this behavior can explain the threshold we observe at 50 kg for yellowfin/albacore/bigeye. Over this size, the schooling behavior can be different. As Partridge *et al* (1983) said, if the prey schools structure is primarily organized to facilitate anti-predator tactics, then one might expect predatory schools to be organized on quite different principles. Sharp (1981) also distinguished prey fish benefit and predator benefits from schooling. To hunt fast-swimming preys, tuna can develop new school structures, more easily made while the number of individuals is smaller.

The previous assumptions support the contention that school size is an adaptation of fish for hunting high speed preys. The foraging theory, and precisely the ideal free distribution, can help us to give some explanations to the following result: that school size would be a result of a foraging behavior. The ideal free distribution describes the possible distribution of the animals in heterogeneous habitats. The principle of this model is that if individuals are "free" to move to alternative patches without any constraint or restriction, then "ideally" each individual goes to the place where its gains will be highest. When the individuals have different competitive abilities, we tend to have the << truncated phenotype distribution >> (Milinski and Parker, 1991) They take individuals of the same species but of various sizes, in habitats in which the patches profitabilties depend on the individual size. In some patches, the competitive weight of the largest competitors is not much different from that of the smallest competitors. That is, the largest competitors do not have any advantage relative to small competitors. In other patches, the biggest competitors do much better than small ones. We also find intermediate patches. From this model, the largest competitors should be found in patches where the effects of size are most critical. The smallest competitors occur in the patches, where the effects of the size are least important, and the medium-sized competitors occur in the intermediate patches. The group size depends on the type of the patch and the profitability of each patch. So, the type of prey can determine the group size. According to this result and to the previous remarks about the changes in food preference for tuna, we can advance that individual size acts on school size. Picher (1986) considers that the assumptions of this model cannot occur because there are constraints for a fish, so the assumptions of the ideal free distribution model are not checked. But we wonder whether the constraints were compared with the needs of fish. We can expect that the constraints exist but they do not really act on the behavior because of the high necessity to find energy. However, we only have assumptions here to better understand this phenomenon.

After these assumptions from statistical analysis on purse seiner data, a next step would be to make models and to develop ethological observations to examine these assumptions. Paradoxically, it appears that few studies have tried to test the ideal free distribution assumptions and predictions with data from real life. Perhaps this preliminary study is a first step to continue to understand the tuna schooling behavior in a new way, based on the ideal free distribution model.

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Table 1: Pairwise comparisons for yellowfin/albacore/bigeye (tonnage). Probability of getting a larger value of Chi^2 under H0 according to Wilcoxon rank-sum (W) and Median test (M).

The overall tests are:
(W):Chi2 = 471.58 (4ddl) (probability > Chi^2) = 0.0001
(M):Chi2 = 700.30 (4ddl) (probability > Chi^2) = 0.0001

weight classes	< 3 kg	3-10 kg	10-30 kg	30-50	>50 kg
< 3 kg		W:0.527 M:0.218	W:0.023 M:0.045	W:0.0001 M:0.0001	W:0.0001 M:0.0001
3-10 kg			W:0.0001 M:0.0001	W:0.0001 M:0.0001	W:0.0001 M:0.0001
10-30 kg				W:0.0001 M:0.0001	W:0.0001 M:0.0001
30-50 kg					W:0.520 M.0.1333

Table 2: Pairwise comparisons for yellowfin/albacore/bigeye (Numbers of individuals). Probability of getting a larger value of Chi^2 under HO according to Wilcoxon rank-sum (W) and Median test (M).

The overall tests are
(W):Chi2 = 409.07 (4ddl) (probability > Chi^2) = 0.0001
(M):Chi2 = 559.60 (4ddl) (probability > Chi^2) = 0.0001

weight classes	< 3 kg	3-10 kg	10-30 kg	30-50	>50 kg
< 3 kg		W:0.0001 M:0.0001	W:0.0001 M:0.0001	W:0.0001 M:0.0001	W:0.0001 M:0.0001
3-10 kg			W:0.0001 M:0.0001	W:0.0001 M:0.0001	W:0.0001 M:0.0001
10-30 kg				W:0.3038 M:0.8589	W:0.0001 M:0.0001
30-50 kg					W:0.0001 M.0.0.0001

Table 3: Pairwise comparisons for skipjack (tonnage). Probability of getting a larger value of Chi^2 under HO according to Wilcoxon rank-sum (W) and Median test (M).

The overall tests are:
(W):Chi2 = 20.1 (4ddl) (probability > Chi2) = 0.0005
(M):Chi2 = 29.9 (4ddl) (probability > Chi2) = 0.0001

weight classes	< 1.8 kg	1.8-4 kg	4-6 kg	6-8	> 8 kg
< 1.8 kg		W:0.0001 M:0.0007	W:0.0001 M:0.0001	W:0.0108 M:0.0139	W:0.0005 M:0.0002
1.8-4 kg			W:0.0004 M:0.0257	W:0.2190 M:0.2290	W:0.4790 M:0.2342
4-6 kg				W:0.710 M:0.486	W:0.0015 M:0.108
6-8 kg					W:0.186 M.0.137

Table 4: Pairwise comparisons for skipjack (Numbers of individuals). Probability of getting a larger value of Chi^2 under HO according to Wilcoxon rank-sum (W) and Median test (M).

The overall tests are
(W):Chi2 = 121.97 (4ddl) (probability > Chi2) = 0.0001
(M):Chi2 = 277.70 (4ddl) (probability > Chi2) = 0.0001

weight classes	< 1.8 kg	1.8-4 kg	4-6 kg	6-8 kg	> 8 kg
< 1.8 kg		W:0.2496 M:0.8978	W:0.0211 M:0.0004	W:0.1532 M:0.6521	W:0.0001 M:0.0001
1.8-4 kg			W:0.0003 M:0.0631	W:0.2974 M:0.6419	W:0.0001 M:0.0001
4-6 kg				W:0.7705 M:0.8754	W:0.0001 M:0.0001
6-8 kg					W:0.0121 M.0.0426

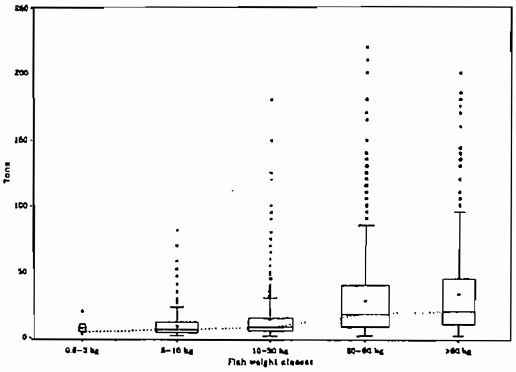

Fig. 1: Evolution of school size (t) with individual fish weight Yellowfin/albacore/bigeye

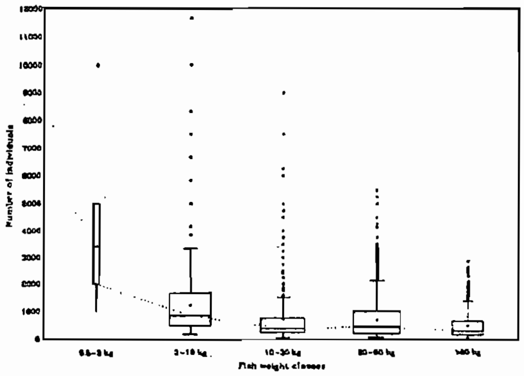

Fig. 2: Evolution of school size (number of individuals) with individual fish weight - Yellowfin/albacore/bigeye

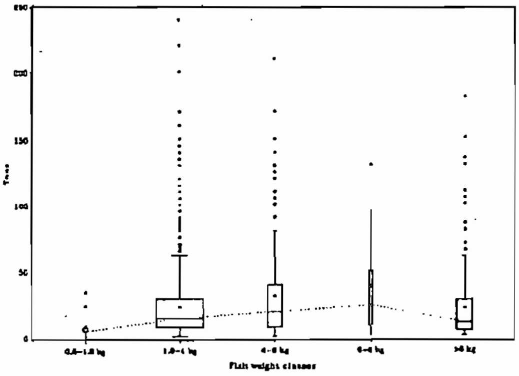

Fig. 3: Evolution of school size (t) with individual fish weight Skipjack

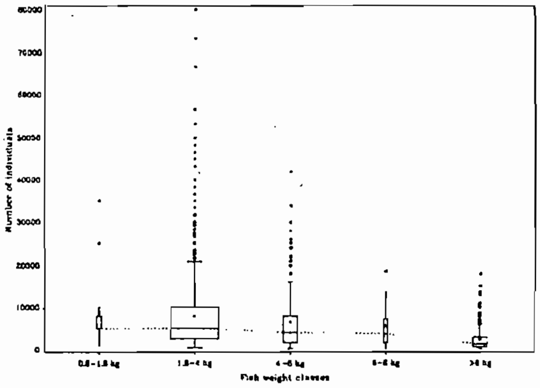

Fig. 4: Evolution of school size (number of individuals) with individual fish weight Skipjack

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