Density-dependent size selectivity in Antillean fish traps

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Abstract

Size selection in fish traps is often considered to depend only on mesh size and fish length. A fishery-independent trap survey conducted in three islands of the Lesser Antilles showed important differences in location of the left arm of the length–frequency distribution (selection profile, and average selection lengths L_{50}) among sampled sectors, in spite of standardized gear and processing methodology. Differences in size structure of the populations could cause such gaps only in sets of conditions which are highly unlikely, if not impossible, in real situations. Differences in the selection process (probability for a fish to be retained by the mesh) are, therefore, thought to be the factors explaining these observations. The inverse relation between the average catch/trap and the shift of the selection profile strongly suggests that fish escapement through the mesh by squeezing is a density-dependent process, which confirms previous observations by other researchers. © 1998 Elsevier Science B.V. All rights reserved.

1. Introduction

In the Caribbean region, where the generally rough bottoms (either coralline or rocky) preclude the use of towed gears, traps are the main gear for demersal fishing and represent a large part of both fishing effort or activity and groundfish landings (Mahon, 1993; Appeldoorn and Meyers, 1993; Aiken, 1993); these traps are traditionally built with natural materials (bamboo, or other woods) but increasingly with wire-mesh netting (Guillou and Lagin, 1997), and catch a wide variety of fish of generally small to moderate size (Gobert, 1994). Although the quantitative stock assessment methods are still very difficult to apply in small-scale multigear and multispecific fisheries, it is

generally considered that the reef fish resources are fully exploited in most parts of the Caribbean and even severely overfished in some islands (Mahon, 1993; Appeldoorn and Meyers, 1993; Aiken, 1993). In spite of the recognition that the increase of fishing effort involves several types of gear, and of the general opposition to the use of trammelnets (Gobert, 1992), the importance of traps has put this particular fishery on the front of the stage. In Bermuda, the situation was felt critical enough to lead the government to close it in 1990 (Butler et al., 1993), but in most other Caribbean countries the regulation is based on minimum trap mesh sizes ranging from 31 to 45 mm (Chakalall, 1995). Mahon (1990) states 1.5″ (38 mm) as a possible short-term (3–10 years) regulation objective for the trap fishery.

Studies on the mode of operation of fish traps were initially directed on the performance of the gear and

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the way catch builds up (High and Beardsley, 1970; Munro et al., 1971; Munro, 1974; Stevenson and Stuart-Sharkey, 1980; Luckhurst and Ward, 1987). More recently, much work was done on the size selectivity of traps (Moran and Jenke, 1990; Sutherland et al., 1991) and its description with a trawl-type sigmoid model as suggested by Pope et al. (1975) (see also Ward, 1988; Chevaillier, 1990). In such a model, mesh size and fish length are, of course, the main factors determining the probability of capture, but other factors may also affect the selection process: for trawls, Pope et al. (1975) mention the type of material and the use of extra netting on cod-end. In the case of fish traps, whose selectivity is still poorly described compared to that of trawls, the nature and impact of such factors are still unknown; however, their existence is strongly suggested by observations showing that simple selection models based on mesh size and fish length do not fully account for the length structure of the catch (Hartsuijker and Nicholson, 1981; Ward, 1988). This paper presents results of standardized trap fishing experiments in the Lesser Antilles, where differences in catch-length structure among areas confirm these earlier findings and suggest that selectivity is related to fish abundance.

2. Methodology

2.1. Data collection

Within a wider research program focusing on demersal resources and fisheries in the Lesser Antilles, fishery-independent surveys were conducted in 1991–1993 in three of these islands, using a standardized fishing technique based on Antillean fish traps.

Five sectors were fished (Fig. 1), on both leeward (west) and windward (east) shelves of Guadeloupe (GE and GW), Dominica (DE and DW) and Martinique (MA). Traps were set within bathymetric strata on the shelf, from ca. 10 to 70 m; the depth distribution of trap hauls did not differ widely among sectors. Owing to various constraints, the surveys took place in different periods in each of the three islands: December 1991–December 1992 in Martinique, January–September 1993 in Guadeloupe, and April–October 1993 in Dominica. No quantitative measurements of current strength or other environmental parameters
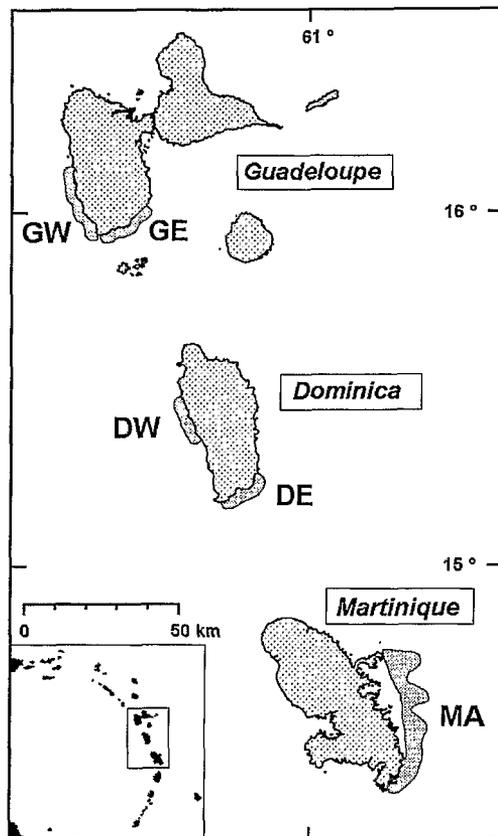
Fig. 1. Map of the sectors sampled in the trap survey.

were done, as they are not known to directly influence the mesh selectivity of fish traps.

The traps used in all sectors were identical in shape (arrowhead with a single funnel) and size (Fig. 2a), building materials (hexagonal wire-mesh on a wooden or metal frame), and mesh opening (31 mm minimal aperture, Fig. 2b). The entrance funnel was opening downward and its aperture was roughly ellipsoid in shape, 15–20 cm wide and 30–35 cm long. Traps were set without bait and were planned to be hauled after one week but due to practical conditions, soak time was much more variable. Practical considerations put a limit to the technical standardization of fishing operations themselves, but the differences (traps set alone or in groups, etc.) are considered to have no impact on the size structure of the catch.

For each trap hauled, the following information on fishing operations was recorded: date, time, position,

a

2.0 m

0.7 m

2.5 m

b

14.2 mm

44.6 mm

30.9 mm
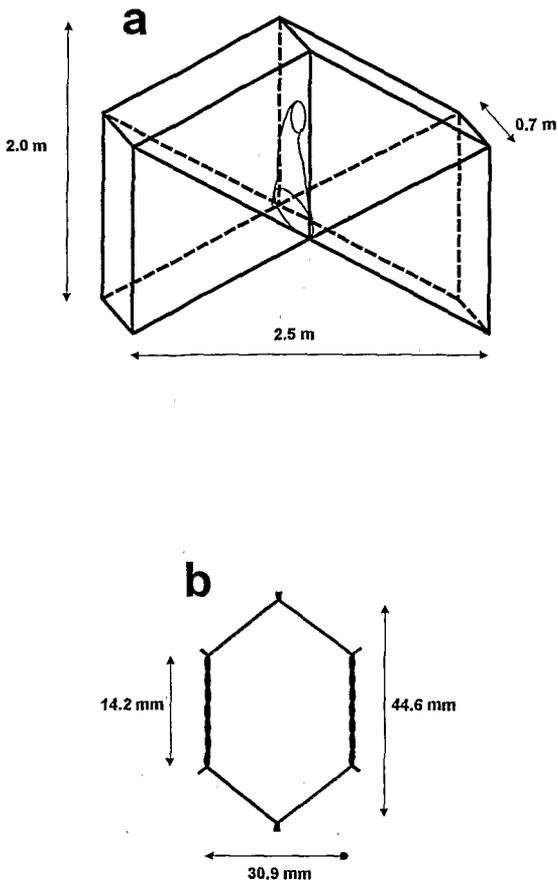
Fig. 2. Shape and dimensions of (a) the arrowhead traps and (b) the hexagonal meshes. The trap is seen from below, standing on its side; the funnel entrance is directed downward.

depth, soak time, as well as the occurrence of any incident. Total length (TL) was measured for each individual fish of the catch, sometimes complemented by fork length (FL) when morphometric relationships were missing. However, in a few isolated cases (such as very large catches), the individual lengths could not be measured exhaustively. Sizes were measured in centimeters or millimeters, but converted in centimeters for the analysis. Numbers of fish measured in each sector are 2372 (DE), 1056 (DW), 4330 (GE), 6935 (GW), 6879 (MA).

2.2. Data processing

The length–frequency distributions used to study selectivity for various species included all fish actually measured in each sector; pooling samples over time and depth allowed keeping sufficient sample sizes and was possible because these two factors were found to have a negligible impact on the length–frequency distributions of a given sector, even for the species with the largest samples.

The logistic selectivity function was fitted to the data with the method based on the catch curve (Pauly, 1984; Sparre and Venema, 1996), using the FAO-ICLARM FISAT software. The estimation process was not impeded by the poor knowledge of the biological parameters (K and L_∞ of the Von Bertalanffy growth function, and natural mortality coefficient M), as it is almost insensitive to K and M, and L_∞ has a negligible impact as long as it is larger than the maximum length in the sample.

Average catch in weight and number in each sector was computed with the log-normal estimator (Dagnelie, 1973) on non-empty traps hauled after 6–9 days. Rejecting data from traps hauled empty was justified by the high probability for these traps to have fished in abnormal conditions (fallen upside down or door left open), and selecting soak times from 6–9 days was necessary because of the wide dispersion of values (from 4 to >60 days). Average catch data from sector DW were not included as there are clear signs of traps having been hauled by fishermen in spite of the use of delayed float release ('pop-up') systems. However, this is not thought to have impacted upon the length composition of the catch, at least in the length ranges considered here.

3. Results

3.1. Observations on length–frequency distributions

For most species, the left-hand, ascending part of the length–frequency curve (called selection profile in what follows) lies between 10 and 20 cm TL. The individual profiles (one species, one sector) differ among species, according to differences in body proportions (length-to-height ratio), but also among sectors for a given species, which is more unexpected, given the standardization of the fishing gear. Whereas the profiles are generally very similar in shape, there is often a gap of at least 1 cm among sectors, and even much more for some species, among which *Holocen-*
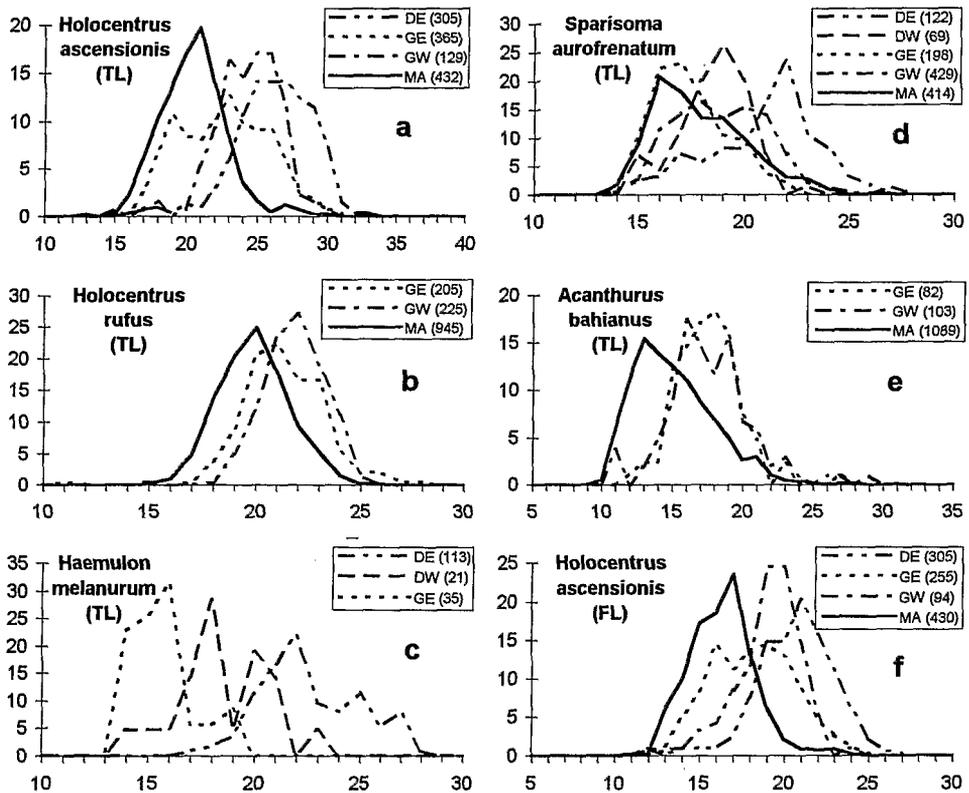
Fig. 3. Length-frequency distributions in total length for (a) *Holocentrus ascensionis*, (b) *H. rufus*, (c) *Haemulon melanurum*, (d) *Sparisoma aurofrenatum*, (e) *Acanthurus bahianus*, and (f) in fork length for *Holocentrus ascensionis*. Lengths are in centimeters and relative frequencies in %. Numbers between parentheses in the legends indicate sample sizes.

trus ascensionis (5 cm), *H. rufus* (3 cm), *Haemulon melanurum* (5 cm), *Sparisoma aurofrenatum* (4 cm), *Acanthurus bahianus* (3 cm) (Fig. 3a–e).

The sectors were first ranked qualitatively by comparing the respective position of the profiles on the length–frequency graph (higher, lower, or approximately equal); this is obviously somewhat subjective but can be applied to more species than the quantitative approach. Fourteen species could be compared, providing results presented in Table 1.

A more quantitative approach involved fitting a sigmoid selection curve to each length distribution whose sample size was large enough, and provided an estimate of the mid-selection length (L_{50}), where the probability of selection is equal to 0.5. (Tables 2 and 3).

These two approaches lead to a consistent ranking of sectors: selection always occurred at the largest

length in sector DE and almost always at the lowest in sector MA, while the other three lie between, so that the overall pattern is the following: DE–GW–DW–GE–MA. Since all sectors were sampled with the same gear used in almost identical conditions in all sectors,

Table 1
Summary of qualitative comparisons of selection profiles between sectors: numbers of species for which selection in sector S1 occurs at lengths higher than (bold), approximately equal to (normal), or lower than (italics) selection in sector S2

Sector S1	Sector S2				
	DE	GW	DW	GE	MA
DE	—	**4**,0,*0*	**1**,0,*0*	**4**,0,*0*	**4**,0,*0*
GW	0,0,*4*	—	0,1,*0*	**8**,4,*2*	**12**,1,*0*
DW	0,0,*1*	**0**,1,*0*	—	**1**,0,*0*	**1**,0,*0*
GE	0,0,*4*	**2**,4,*8*	0,0,*1*	—	**8**,5,*0*
MA	0,0,*4*	0,1,*12*	0,0,*1*	0,5,*8*	—

Table 2
Selection length (L_{50}) of the species–sector distributions for which the selection curve could be fitted

Species	Estimated values of L_{50}					Maximum difference		Model L_{50} [b]
	DE	DW	GE	GW	MA	sectors	value	
Holocentrus ascensionis	24.3		22.3	24.3	20.9	DE–MA	3.4	19.9
Holocentrus rufus			20.4	21.3	19.9	GW–MA	1.4	21.2
Sparisoma aurofrenatum	22.3		16.2	17.9	16.6	DE–GE	6.1	15.8
Haemulon flavolineatum [a]			16.0	19.2	16.7	GW–GE	3.2	
Pseudupeneus maculatus			20.7	21.2	20.9	GW–GE	0.5	22.0
Myripristis jacobus		15.0	14.4	15.6	14.5	GW–GE	1.2	15.0
Haemulon aurolineatum			18.0	17.9	17.4	GE–MA	0.6	18.5
Mulloidichthys martinicus			22.4	21.7	21.6	GE–DE	0.9	24.0
Lutjanus synagris			17.9	19.0		GW–GE	1.1	17.3
Haemulon plumieri			20.6	17.3		GE–GW	3.2	15.2
Haemulon chrysopterum			18.9	17.1	16.6	GE–MA	2.3	

[a] Fitting was poor for *H. flavolineatum*.
[b] Model L_{50} is the selection length estimated by Chevaillier (1990).

these differences may be the effect of data collection and sampling, size structure of sampled populations, or selection processes.

3.2. Effect of data collection methodology and sampling

The choice of total length as the measurement standard for fishes is sometimes questioned as it may lead to errors in long- and thin-tailed species such as squirrelfishes (Holocentridae). However, most species have unambiguous total length measurements, and the difference in selectivity profiles is observed also with fork length distributions, as shown by the example of *Holocentrus ascensionis* (Fig. 3f). Possible observer-related biases in fish measurement methodology can also be ruled out by the observation that

Table 3
Summary of quantitative comparisons of L_{50} between sectors. Numbers of species for which L_{50} of sector S1 is higher (**bold**) or lower (*italics*) than L_{50} of sector S2.

Sector S1	Sector S2				
	DE	GW	DW	GE	MA
DE	—	**2**,*0*	**0**,*0*	**2**,*0*	**2**,*0*
GW	**0**,*2*	—	**1**,*0*	**6**,*4*	**8**,*0*
DW	**0**,*0*	**0**,*1*	—	**1**,*0*	**1**,*0*
GE	**0**,*2*	**4**,*6*	**0**,*1*	—	**5**,*3*
MA	**0**,*2*	**0**,*8*	**0**,*1*	**3**,*5*	—

differences were found between east and west sectors of Guadeloupe (GE and GW), where all field and laboratory work was done in the same conditions by the same persons.

Even though the smallest samples were excluded from the analysis, their sizes are generally quite low, which could be thought to weaken the observations. However, the sampling variability does not seem to have produced irregular-shaped distributions, and the clearest observations were made on the largest samples collected (up to >1000 fish).

It is, therefore, concluded that the observed differences are not attributable to data collection and really reflect the length structure of the catch.

3.3. Effect of size structure of the sampled populations

If the selection function (probability for a fish present within the trap to be retained in the catch) is the same in all sectors, then length–structure differences of the populations are the only possible origin of those of the catch. However, it will be shown with a trap selection model that, for a given selection function, a significant shift in the selection interval into the catch (as observed here) would require the population structure to have very unrealistic features. The trap selection model is $C(l) = p(l)N(l)$, where l denotes fish length, $C(l)$ the number of fish caught, $p(l)$ the logistic selection function, and $N(l)$ the number of fish which
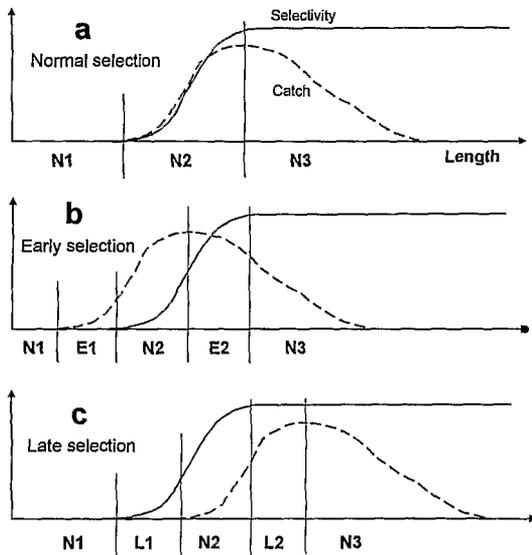
Fig. 4. Theoretical graphs of respective positions of selection curve and catch length–frequency distribution (X-axis, length; Y-axis, frequencies and probabilities).

entered the trap (Chevaillier, 1990). The increasing or decreasing variation of the catch when length increase is shown by the sign of the derivative of $C(l)$: $dC/dl = p\,dN/dl + N\,dp/dl$.

In the normal case, where catch frequencies increase in the same interval as the selection probability, the length range can be divided in three intervals (Fig. 4a):

- N1: the selection probability $p(l)$ is too close to 0 to allow any fish to be caught in the sample;
- N2: the increase in selection probability is large enough to compensate for the decrease in numbers; and
- N3: the selection probability is very close to 1, and the decrease in catch follows the decrease in numbers.

When there is a gap between selection and catch ('early' or 'late' selection, Fig. 4b and c), other intervals (E1, E2, and L1, L2) must be added to the three already defined (N1, N2, N3) to describe the whole pattern:

- E1: fish are caught in non-negligible numbers although selection probability is still very close to 0; this is possible only if $N(l)$ takes very high

values, which are incompatible with its definition as the number of fish which entered the trap (and not the number in the population).

- E2: the numbers caught decrease ($dC/dl<0$) although selection probability is still increasing ($dp/dl>0$); this implies that $N(l)$ is either close to 0 (to offset the increase of $p(l)$) or decreasing very sharply (dN/dl negative with very large absolute value). Such a sharp decrease is not likely within a few length-classes; furthermore, it would lead to zero numbers in subsequent classes, which is not the case.

- L1: in spite of non-zero selection probability, no fish is still caught; this is possible only if $N(l)=0$, i.e. although present in the population, no fish at all enters the trap in this length interval. No size-related behavioral factor has been shown in reef fish species, which would account for the situation required here.

- L2: catch numbers continue to increase ($dC/dl>0$) above the full selection length, i.e. when selection-probability increase is negligible ($p\approx1$, $dp/dl\approx0$). $N(l)$ has to be very large, or (possibly, and) its variation (dN/dl) has to be positive or weakly negative. This is most unlikely, as very large values of $N(l)$ are impossible (cf. E1), and an increase or even a slight decrease of numbers as length increases is not usually found in fast-growing reef fish whose length–frequency distributions are most often unimodal, especially as they are exploited by a fishery.

Each of these four cases is impossible or very unlikely in real situations. It is thus concluded that, if the selectivity function for a given species is the same in all sectors, the length structure of the exploited populations cannot account for the differences observed repeatedly in length structure of the catches.

3.4. Effect of selection process

It therefore appears that these gaps are related to differences in the selectivity function $p(l)$ among sectors. For a given species, this function is generally assumed to be dependent only on the characteristics of the fishing gear (but see Pope et al., 1975); in the present case, some other factor determines the differ-

ences among sectors. The selectivity function $p(l)$ is the probability for a fish that entered the trap to be present in the final catch when the trap is hauled.

Three cases could prevent this event from being realized:

- The fish escapes from the trap by the funnel: this is known to occur as a normal component of the mode of operation of traps (Munro, 1974). In the present case, the opening of the funnel is much larger of the section of most fish caught, even more than those within the selection interval: with respect to this interval, escapement through the funnel can be considered as a size-independent process which cannot explain differences in selectivity among sectors.
- The fish is eaten by a predator within the trap: the only piscivorous species caught in non-negligible numbers and capable of eating fish of the size considered here (Randall, 1967) are morays eels (mainly *Gymnothorax spp*). Fish recently ingested were observed in a few occasions when processing the catch in the laboratory, and scars or injuries showed evidence of predation attempts by morays; earlier thus undetectable, digestion of prey eaten within the trap can, therefore, be thought to have occurred more often. The frequency of occurrence as well as the average number of morays caught by trap lead to a ranking of sectors only partly matching that of the selection profiles (Table 4). This fact, and the only limited size-dependence of predation by morays, suggests that it may not be the main factor responsible for the shift in selectivity pattern. According to Munro et al. (1971), predation by moray eels is probably much more important in traps lost for one month or more in the water, than in the normal operation of the gear after a few days of soak.

- The fish escapes through the mesh openings: this is the *stricto sensu* definition of trap mesh selectivity and the normal process determining the retention probability, through the relationship between the maximum opening of the mesh and the body height of the fish (Chevaillier, 1990). In addition to the variability of mesh dimensions and fish length-to-height ratio, the possibility of some squeezing of the fish body accounts for the sigmoid shape of the selection curve and its experimental variability. That fish of a given species and length have different escapement probabilities in different areas suggests that the factors responsible for the exit through the meshes (called here 'exit pressure') are dependent on the characteristics of the populations. Although the traps were quite large (2.2 m^3), the number of fish present inside could be one of such factors (Table 5).

The average weights show wide differences among sectors, all of which are highly significant (Student t-test, $p < 0.01$) except the last one (GE–MA: $t = 0.85, p = 0.39$), and which lead to the same ranking order as the selectivity profiles. This suggests that the abundance of fish inside the trap could be acting on the exit pressure. The number of individuals per trap varies very little among sectors (except for sector GW) when all lengths are considered, but the largest fish are several times more abundant in DE than in MA, with intermediate values for the Guadeloupean sectors. According to this criterion, the ranking order of the four sectors is consistent with that of the selectivity profiles, thus implying that the presence of large fish is more important than the total number to induce in small fish a fleeing behavior by forcing their way out through the meshes.

Table 4
Summary of moray eel (*Gymnothorax spp*) catch characteristics in the non-empty traps

	GW	DE	DW	MA	GE
% of traps having caught moray eels	25.2	21.1	12.5	9.1	7.7
Average number of moray eels caught per trap	0.50	0.29	0.15	0.17	0.11

Table 5
Average weight and numbers of individuals per trap (non-empty traps hauled after 6 to 9 days)

	DE	GW	GE	MA
Average weight (kg)	4.93	3.34	2.36	2.33
Average number of individuals	17.99	18.59	11.57	18.48
Average number of individuals larger than 30 cm TL	3.16	0.91	1.07	0.52
Average number of individuals larger than 40 cm TL	1.11	0.54	0.33	0.21
Average number of individuals larger than 50 cm TL	0.43	0.46	0.28	0.18

4. Discussion

The existence of differences in trap selectivity patterns was suggested by previous observations of either discrepancies between catch size structure and selection models (Hartsuijker and Nicholson, 1981; Ward, 1988), or gaps among length frequencies collected in various areas (Munro, 1983).

Ward (1988) discussed various possible causes for the observed differences between observed and predicted values of L_{50} and could only speculate, because of lack of experimental data, that behavioural factors related to fish size or to the presence of aggressive species (such as *Balistes vetula*) could increase the escapement rate of small fish by 'squeezing' through the rigid meshes. A similar problem is found in the present study, where the observed selection patterns are not always consistent with those established by Chevaillier (1990) (Table 2) in one of the fishing areas (eastern shelf of Martinique).

The observations of Munro (1983) were of a different nature, as there was no reference to a selection model, but differences between observed size structures from various areas. Noticeable gaps were found for many species between length distributions from coastal and heavily exploited areas (Port-Royal Reefs) and offshore unexploited areas (Pedro Bank), with larger fish always caught in the latter area. Possible causes were supposed to be the size structure of populations (absence of either small or large fish from the fishing area) and the rate of exploitation (in coastal areas, the fish would be eliminated by the fishery before having reached the full selection size). The ability of fish to force an exit through the mesh is mentioned, but the discussion generally deals with the whole size structures rather than the selection profile itself.

In the present case, the strict standardization of fishing gear and the close ecological similarity of the five areas (shelf of high volcanic islands) strongly support the existence of different selection processes. No direct observation of fish escapement could be made in this field study, but the aquarium experiments of Sutherland et al. (1991) have shown that reef fish are able to force their way through the mesh, even bending and distorting it in their efforts to escape, thus confirming the squeezing hypothesis of Ward (1988). The relation of escapement with fish abundance within the trap (and therefore in the population) is suggested by the matching of sector rankings by both criteria, which was also found very clearly in Jamaican trap survey data (Munro, 1983).

The shift of selection length toward smaller values when fish abundance decreases entails two consequences which, although probably of moderate importance, are worth mentioning. First, because of the higher probability of escapement of small fish in populations with higher density, the catch per unit effort (CPUE, e.g. kg/trap) is, in a way, underestimated; put differently, and assuming that CPUE in traps is proportional to density, the range of densities in populations fished by a trap survey is wider than shown by the CPUE. A second consequence of this density-dependent selectivity pattern is that the more heavily a population is exploited, the smaller the fish are likely to be caught within the selection interval: the two components of the fishing pressure (selection and effort) add their effects.

Acknowledgements

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