Trophic flow kinetics in marine ecosystems: Toward a theoretical approach to ecosystem functioning

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ABSTRACT

Based on a theoretical approach, Gascuel showed that trophic flow kinetics is a key characteristic of ecosystems' functioning, partly determining their response to human disturbances such as fishing pressure. The kinetics quantifies the speed of the trophic flow, i.e., the velocity of biomass transfers from low to upper trophic levels, due to predation and/or ontogeny. In the present paper, we show that the production/biomass (P/B) ratio, used in many ecosystem models and particularly in the EwE software, can be considered a measure of this speed of the trophic flow. We propose an empirical model that expresses the P/B ratio as a generic function of the trophic level (τ) and the mean water temperature (θ).

The model was fitted to two datasets. The first was extracted from FishBase and includes 162 unexploited fish stocks for which the required parameters were available ($P/B = M$, τ and θ). In that case, the model represents transfer kinetics in fish communities as $P/B = 2.31\tau^{-1.72} \exp(0.053\theta)$ ($R^2 = 0.37$). It is consistent with estimates of natural mortality M based on FishBase data and Pauly's empirical equation ($n = 5258$). Additionally, a model explains 68% of the total variance is proposed, which links P/B ratios to the trophic level and to the von Bertalanffy growth coefficient, K. The second dataset included 1718 groups from 55 published Ecopath models. Here, the model expresses the mean trophic flow kinetics through all groups, from primary producers to top predators, as $P/B = 20.19\tau^{-3.26} \exp(0.041\theta)$ ($R^2 = 0.54$). A negative size effect is shown, with faster transfers occurring in young and less productive ecosystems. Transfers faster than mean are also observed in upwelling ecosystems and for zooplankton, while slower flow characterize benthos, marine mammals and birds. A relationship between trophic level and time (t) was finally deduced from the P/B model. It expresses the trophic level reached at time t by a unit of carbon fixed in the food web by primary producers at time $t = 0$.

Considering the P/B ratio a measure of the trophic flow kinetic provides a new way to look at this parameter. Implications of the model are discussed and its usefulness for building a general theory on ecosystem functioning is argued. We especially discuss how changes in the flow kinetics may contribute to top-down regulations and why fast transfer through the food web is a factor of ecosystems' resilience.

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1. Introduction

In the face of worldwide overfishing of marine resources, the development of an Ecosystem Approach to Fisheries is commonly recognized as one of the major scientific tasks of the 21st century. In that context, a general consensus has now emerged in the community of fisheries scientists that studying trophodynamics is of major concern to improve understanding of marine ecosystem functioning, and to analyse and simulate the impact of fishing at the ecological community scale (e.g., Pitcher and Cochrane, 2002; Cury et al., 2003). The most widely used software for ecosystem modelling is presently EwE (Ecopath with Ecosim, Christensen and Pauly, 1992; Walters et al., 1997), which is based on a representation of biomass flows due to predation between 'trophic boxes' representing individual species or aggregated species characterized by similar prey and predators. Related to this, Gascuel (2005) developed a theoretical model of trophic flow, which is complementary to the Ecopath approach, and has been named EcoTroph. Based on two main differential equations, one regarding biomass flow and the other related to flow kinetics, this model quantifies in a continuous way the transfers of production related to predation and ontogenetic changes, in a trophic network from secondary production to top predators. This approach leads to a theoretical representation of the functioning of marine ecosystems. It particularly shows that trophic flow kinetics is a key characteristic, partly determining the ecosystems' response to human disturbances such as fishing pressure.

Theoretically, the trophic kinetics may be quantified by the speed of the trophic flow, which measures the velocity of transfers from low to upper trophic levels, due to predation and/or ontogeny. In practice, estimating the speed of the trophic flow appears non-trivial and this parameter never seems to have been measured as such. Thus, in the EcoTroph theoretical approach, empirical values based on reasonable but arbitrary considerations were used for the simulations (Gascuel, 2005). This appeared sufficient to build or analyse general rules, but the theoretical basis of the model remained rather weak. Additionally, in a first attempt to apply a reverse form of the EcoTroph model to real case studies, in order to estimate ecosystem biomass using catches as input, it was found that underestimating the speed of the trophic flow constitutes a clear limit for the model implementation (Gascuel and Chassot, 2008). More generally, quantifying flow kinetics appears as a key step in our understanding of ecosystems dynamics.

In the present paper, our main goal is, thus, to determine the general shape of the flow kinetics model, i.e., to quantify the relationship between the speed of the flow and the trophic level. It is first shown that the production/biomass (P/B) ratio, used in many ecosystem models and particularly in the EwE software, can be considered a measure of the speed of the trophic flow, based on the assumption that the transfers of production mainly result from predation. This allows us to propose a model which links flow kinetics to both the trophic level and the water temperature. Fitting the model to two datasets, one extracted from FishBase (www.fishbase.org; Froese and Pauly, 2000) and the other built from published Eco-

path models (Morissette, 2007), leads to generic estimates of the speed of trophic flow. We finally argue why quantifying the speed of the trophic flow should constitute a step toward a general theory of ecosystem functioning and fishing impact. We especially discuss the consequences of the slowing of the trophic flow for upper trophic levels, on top-down controls and on ecosystems' resilience.

2. Methods

2.1. The trophic flow kinetics: theoretical approach

EcoTroph was proposed as a theoretical model of ecosystem functioning and impact of fishing (Gascuel, 2005). In this trophic-level-based model, all the biomass of the ecosystem is distributed along a continuum of trophic level values (τ) split into fractional classes. Conventionally, we consider trophic classes of $\Delta \tau = 0.1$ range step, from trophic level 2 corresponding to secondary producers to trophic level 5, the latter considered sufficient to cover almost all top predators. Thus, the distribution of the ecosystem biomass per trophic class is used as a discrete approximation of the continuous distribution. The resulting curve, B as a function of τ, represents a key aspect of ecosystem functioning and constitutes what is called a 'biomass trophic spectrum' (Gascuel et al., 2005).

In ecosystems, biomass moves from lower to higher trophic levels due to growth and predation, as can be best illustrated by the fate of a single particle (e.g., a carbon atom) drawn schematically in Fig. 1 (dotted line). This particle enters the ecosystem at time $t = 0$, through a primary producer at trophic level = 1, for instance a phytoplanktonic organism. Then, it jumps very rapidly to trophic level 2 due to grazing by small zooplankton. It may stay here for a short time, and then be consumed by a fish, e.g., a juvenile sardine. This juvenile sardine will increase its own trophic level, as it graduates, in the course of its ontogeny, from feeding on small, herbivorous zooplankton to feeding on a mixture of small and larger zoo-

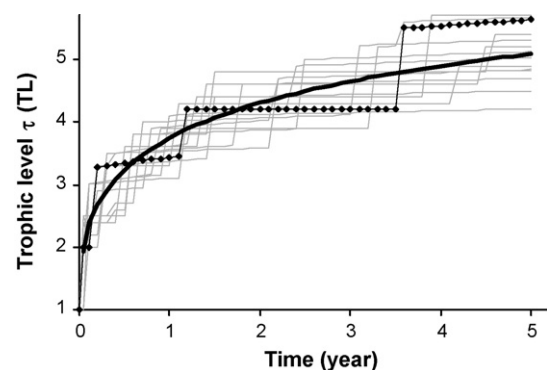Fig. 1 – Illustrating the transition from a discrete to a continuous representation of biomass flow in an ecosystem. Grey broken lines refer to the trajectories of single particles along trophic levels (see text for explanations on the fat of the single particle illustrated by dotted line), while the continuous line refers to the mean trajectory of biomass flow from low to upper trophic levels.

plankton, some of it carnivorous. After, say, a year, this sardine is eaten by an adult cod, with a trophic level of 4.1. This cod will not experience an ontogenic increase of its trophic level, but survive more than two years before becoming the prey of a top predator, whose trophic level is higher than 5.

The fate of our particle is thus characterized by continuous processes (ontogenic changes in trophic levels) and abrupt jumps caused by predation. The example illustrates the specific fate of a given particle, and other particles will have different fates. Yet there are generalities: with the exception of those in semi-autotrophic organisms (such as corals), all of the particles start with photosynthesis or detritus recycling at trophic level 1; from there, they move up more or less rapidly, jumping for each predation event to a trophic level, which is defined by the mean diet of the predator. Few particles, however, reach the highest trophic levels, and most will stop long before that, due to non-predation mortality, excretion or respiration. The particles that move up the food web have a wide range of trajectories, as illustrated in Fig. 1 (grey lines). As a consequence, the flow of particles can be considered a continuous process. In fact, the continuous model (solid black line in Fig. 1) is not an approximation of the discrete process. It is the mean process itself, expressed as a flow of biomass. This is the key idea of EcoTroph: the trophic functioning of marine ecosystems can be modelled as a continuous flow of biomass surging up the food web, from lower to higher trophic levels.

Therefore, biomass can be considered as 'flowing' through each trophic level. Herein, 'flow' (also called 'biomass flow') refers to the amount of biomass that moves up the food web, which can be expressed in tonnes per year (t year^{-1}) or equivalent units for any trophic level. Obviously, this flow decreases from low to high trophic levels, due to respiration and non-predation mortality. On the other hand, the trophic flow is also characterized by a speed, which measures the kinetics of the process. In other words, each of the particles starting at a trophic level of 1, and therefore biomass itself, reaches the upper levels after a certain time. Thus, the speed of the biomass flow quantifies the velocity of biomass transfers in the food web. This speed can be expressed in terms of the number of trophic levels passed per year (TL year^{-1}).

Finally, the quantity of biomass, present at any moment in a given trophic class, can be deduced under steady-state conditions from both the biomass flow and the flow kinetics. As in hydrology, where the quantity of water in a given canal length can be calculated as the flow (e.g., in l s^{-1}) divided by the flow speed (m s^{-1}), the amount of biomass in a trophic class of $\Delta\tau$ wide range is:

$$B_\tau = \frac{\Phi_\tau}{d\tau/dt}\Delta\tau \qquad (1)$$

where Φ_τ is the mean biomass flow through the trophic class τ (in t year^{-1}) and $d\tau/dt$ is the speed of the flow (TL year^{-1}); thus, B_τ is expressed in tonnes.

This EcoTroph approach, based on a continuous representation of the trophic flow, can be compared to the well-known and widely used Ecopath model where biomass is split into various trophic boxes. During each unit of time, each box produces P at trophic level τ, of which a part Q is consumed
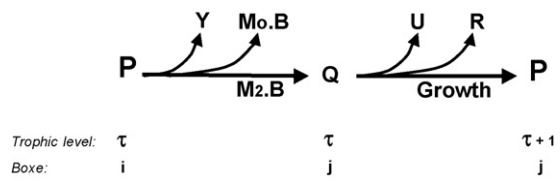

Fig. 2 – Schematic representation of the conceptualisation of biomass flow in Ecopath. The production P of the prey i at trophic level τ is split into three parts: predation ($M_2 B = Q$), losses due to non-predation mortality ($M_0 B$) and fisheries catches ($FB = Y$). Of the amount Q, only a small fraction is transferred by the predator j from trophic level τ to $\tau + 1$, due to losses connected with excretion (U) and respiration (R) (see **Christensen and Pauly, 1992**).

by predators, whose production occurs on average at trophic level $\tau+1$ (Fig. 2). Thus, the production $P(\tau+1)$ constitutes a trophic flow transferred from level τ to level $\tau+1$. It is usually expressed in t year^{-1} but it implicitly refers to a one-trophic level jump. Thus, seen in a continuous perspective, it should be more rigorously expressed in t TL year^{-1}.

Assuming that transfers result only from predation leads to a strong analogy between the two approaches. In both cases, the functioning of ecosystems is represented as a trophic flow moving from lower to upper trophic levels, with losses due to non-predation mortality, catches, excretion and respiration. Therefore, from this analogy, it follows that the production of the trophic class $[\tau, \tau + \Delta\tau]$ is:

$$P_\tau = \Phi_\tau \Delta\tau \qquad (2)$$

From Eqs. (1) and (2) it is finally deduced:

$$\frac{d\tau}{dt} = \left(\frac{P}{B}\right)_\tau \qquad (3)$$

where $(P/B)_\tau$ is the mean P/B ratio observed in the related trophic class.

As a consequence, the P/B ratio observed in a specific box can be seen, in practice, as a measure of the speed of the trophic flow that passes through that box at every moment. This result, which will be discussed in depth later, enables us to build a model that expresses the P/B ratio, and thus the speed of the trophic flow, as a generic function of τ.

2.2. Fitting an empirical model expressing P/B as a function of TL

Quite obviously, the speed of the trophic flow should be a decreasing function of the trophic level. Indeed, metabolism at low trophic levels is generally very fast, involving small organisms belonging to the phytoplankton, zooplankton or micro- and meiobenthos, which exhibit high turn-over. Only few species, such as herbivorous fishes (e.g., rabbitfish of the Family Siganidae, which feed predominantly on seagrass), should constitute exceptions for this general rule. Thus, high metabolism, fast turn-over and short life cycles induce fast trophic transfers from the lowest toward the higher trophic

levels. Conversely, high-trophic level predators are generally large and long-lived, and have few predators. Thus, the trophic flows they mediate should be characterized by slow kinetics.

The temperature of the environment also impacts the metabolism of organisms, biochemical reactions being faster at higher than at lower temperatures. Logically, it should follow from this that trophic kinetics should be particularly fast in warm-water ecosystems. To capture this, an empirical model of the speed of the trophic flow was built, by fitting observed P/B ratios as a function of the trophic level τ and the water temperature θ.

Two sets of "observed" P/B data were used. The first one was extracted from FishBase (www.fishbase.org, Froese and Pauly, 2000) based on the assumption that P/B is equal to the total mortality rate Z under equilibrium assumption (Allen, 1971). In FishBase, we thus selected all the stocks that satisfied the following conditions:

- The value of the natural mortality M was known for an unexploited state (therefore M = Z). These M estimates are based on an age-structured or length-converted catch curve analysis (Allen, 1966; Gulland, 1966), or on the mean length of fishes (method of Powell, 1979). M values that were estimated themselves from an empirical model (e.g., the Hoenig model) were excluded, as well as those referred as doubtful in FishBase.
- The trophic level τ was known, based on a diet analysis or on the mean of the food items; TL estimated only for recruits and grazing fishes (τ = 2) were excluded.
- The temperature θ was known, in the habitat where M and τ has been estimated.

This dataset only refers to fishes and includes the n = 162 stocks for which the required parameters were available (P/B = M, τ and θ).

The second dataset refers to all ecological groups, from primary producers to top-predators. It includes 1718 groups from 55 published Ecopath models, which we selected in order to cover a large variety of marine ecosystems (Table 1). In this case, the P/B ratios were generally estimated as the total mortality rate, Z (Allen, 1971), using catch curve analyses or empirical functions such as Pauly's (1980) equation for finfish or Brey's (1999) relationships for invertebrates. The trophic level of each group was estimated by the Ecopath model itself. For each Ecopath model, we calculated the related mean water temperatures from the Levitus Atlas provided by NOAA (http://www.cdc.noaa.gov/cdc/data.nodc.woa98.html; yearly SST mean), as the average on a polygon covering the area of the model.

For both datasets, various models were tested, based on exponential or power functions. Models were fitted by a maximum likelihood method, assuming a lognormal distribution for residuals. The selection of the final models was based on a criterion of explained variance and on the examination of residuals. Regarding the FishBase data, the sensitivity of the P/B model was analysed according to the method used for estimating natural mortality M and the trophic level τ. In the case of the Ecopath dataset, the potential impact on the P/B model of the various ecosystems' characteristics was

investigated, such as (see Table 1): the type of ecosystem considered, its primary production, its total biomass, and its total system throughput (TST). This last variable is considered a surrogate for the size of the ecosystem in terms of overall activity (Ulanowicz, 1986; Kay et al., 1989) and an indicator of the system's maturity (Odum, 1969; Christensen, 1995). When available, effect of pedigree as a measure of the quality of each Ecopath model (Pauly et al., 2000) was also examined. Finally, the sensitivity of the P/B model to exploitation patterns was analysed, by fitting it to data from nine Ecopath models that have been studied for two periods of time, before and after fisheries development. Thus, it is possible to compare P/B models estimated with reference to low or high fishing rate conditions.

Two additional analyses were conducted based on the FishBase dataset. First, the P/B model was also fitted taking into account growth parameters L_∞ and K as independent variables. In that case, n = 172 because the dataset included 10 sexed stocks with growth parameter pairs. Secondly, in order to analyse the consistency of our estimates with previous approaches, the selected model was also fitted to a dataset (n = 5258 stocks) including all M values that can be deduced from FishBase and Pauly's empirical equation (1980): $M = 0.985 L_\infty^{-0.279} K^{0.6543} \theta^{0.4634}$.

Finally, an equation linking the trophic level τ and the time t may be algebraically deduced from the P/B model. It allows us to estimate the mean age of the biomass observed in an ecosystem at trophic level τ.

3. Results

3.1. Fitting a P/B model to the two datasets

For both datasets, effects of the trophic level τ and of the water temperature θ on the P/B ratios are highly significant (Table 2). Based on the FishBase dataset for unexploited stocks, the effects of trophic level and temperature, as single independent variables, are both highly significant ($p < 0.001$). The P/B ratio may be expressed as a decreasing function of the trophic level using either a power or an exponential function, both expressions leading to very similar results. Nevertheless, in the case of the Ecopath groups, the variance explained by fitting a power function is slightly higher and, especially, residuals examination shows that an exponential expression leads to underestimating P/B for the lowest trophic levels. Thus, a power model seems to be more appropriate.

Conversely, for both datasets the water temperature effect is better taken into account by fitting an exponential function. That also appears consistent with the possibility of nil or negative values for this parameter. Finally, the selected P/B model is expressed as follows:

- For fishes, based on the FishBase dataset:

$$P/B = 2.31\tau^{-1.72} \exp(0.053\theta) \tag{4}$$

- For all marine groups, based on the Ecopath dataset:

$$P/B = 20.19\tau^{-3.26} \exp(0.041\theta) \tag{5}$$

Table 1 – Characteristics of the 55 ecosystems and Ecopath models used as a dataset for fitting the P/B empirical model (the total system throughput TST is in t km^{-2} year^{-1}, and the total biomass B$_{tot}$ in t km^{-2})

Num	Model	Reference	Ecos. type	°C	TST	B$_{tot}$
1	Alaska Gyre	Pauly et al. (1996)	Open sea	5.0	6,938	87
2	Antartica, Eastern Weddell Sea	Jarre-teichmann et al. (1997)	Open sea	0.2	260	17
3	Australia—South East Fishery	Bulman et al. (2006)	Coral reef	17.2	9,422	192
4	Azores	Guénette and Morato (2001)	Open sea	19.0	17,571	174
5	Bay of Bengal	Mustafa (2003)	Gulf–Strait	27.8	4,717	28
6	Bay of Biscay (1970s)	Ainsworth et al. (2001)	Coast–Shelf	13.9	8,422	257
7	Bay of Biscay (1998)	Ainsworth et al. (2001)	Coast–Shelf	13.9	8,412	254
8	Benguela	Shannon et al. (2004)	Upwelling	16.8	19,498	165
9	Bolinao reef	Aliño et al. (1993)	Coral reef	28.4	39,613	1896
10	California upwelling (65–72)	Jarre-Teichmann (1998)	Upwelling	14.3	13,934	110
11	California upwelling (77–85)	Jarre-Teichmann (1998)	Upwelling	14.3	14,052	118
12	Campeche bank	Arreguín-Sánchez et al. (2004)	Lagoon-Bay	26.7	2,047	86
13	Canada-Eastern Scotian Shelf 1980s	Bundy (2004)	Coast–Shelf	9.8	7,669	245
14	Canada-Eastern Scotian Shelf 1990s	Bundy (2004)	Coast–Shelf	9.8	7,124	310
15	Canada-Hecate Strait	Beattie (2001)	Gulf–Strait	9.7	7,377	129
16	Canada-Newfoundland 1900s	Heymans and Pitcher (2002a)	Coast–Shelf	5.6	10,513	415
17	Canada-Newfoundland 1980s	Heymans and Pitcher (2002b)	Coast–Shelf	5.6	7,458	225
18	Canada-Newfoundland 1990s	Heymans (2003)	Coast–Shelf	5.6	6,438	286
19	Canada-Northern Gulf St. Lawrence 1980s	Morissette et al. (2003)	Gulf–Strait	6.0	5,212	319
20	Canada-Northern Gulf St. Lawrence 1990s	Savenkoff et al. (2004a)	Gulf–Strait	6.0	3,916	276
21	Canada-Southern Gulf St. Lawrence 1980s	Savenkoff et al. (2004b)	Gulf–Strait	6.4	4,916	286
22	Canada-Southern Gulf St. Lawrence 1990s	Savenkoff et al. (2004b)	Gulf–Strait	6.4	4,707	296
23	Cantabrian Sea 1994	Sánchez and Olaso (2004)	Coast–Shelf	15.8		
24	Celestun lagoon	Chavez et al. (1993)	Lagoon-Bay	25.7	8,969	430
25	Central North Pacific	Cox et al. (2002)	Open sea	11.5	856	12
26	Chesapeake bay	Walters et al. (2005)	Lagoon-Bay	17.7	23,000	98
27	Chiku lagoon	Lin et al. (1999)	Lagoon-Bay	24.5		
28	Eastern Bering Sea	National Research Council (2003)	Open sea	4.0	6,571	302
29	Eastern tropical Pacific	Olson and Watters (2003)	Open sea	23.7	535	7
30	Estern Pacific, Aleutians	Guénette (2005)	Coast–Shelf	5.4	5,927	151
31	Faroe island 1961	Zeller and Reinert (2004)	Open sea	8.3	6,690	134
32	Faroe Island 1997	Zeller and Freire (2001)	Open sea	8.3	6,655	131
33	Galapagos—Florena rocky reef	Okey et al. (2004)	Coral reef	23.1	94,850	2620
34	Georgia Strait	Martell et al. (2002)	Gulf–Strait	8.8	31,628	806
35	Great Barrier Reef	Gribble (2001)	Coral reef	26.1	10,899	263
36	Greenland—west coast	Pedersen and Zeller (2001)	Coast–Shelf	3.5	3,894	158
37	Guinea 1985	Gascuel et al., unpub. data	Coast–Shelf	26.6	17,048	223
38	Guinea 2003	Gascuel et al., unpub. data	Coast–Shelf	26.6	15,079	202
39	Gulf of Maine—George Bank 1982	Heymans (2002)	Gulf–Strait	9.7	31,425	350
40	Gulf of Mexico Continental Shelf	Arreguín-Sánchez and Manickchand-Heileman (1998)	Coast–Shelf	25.1	2,924	32
41	Gulf of Mexico, 2006	Walters et al. (2006)	Coast–Shelf	25.8	16,458	367
42	Gulf of Thailand	FAO/FISHCODE (2001)	Gulf–Strait	28.3	12,783	110
43	Iceland 1950	Buchary (2001)	Open sea	4.0	35,224	3818
44	Laguna de bay 1968	Delos Reyes (1995)	Lagoon-Bay	28.5	47,784	201
45	Laguna de bay 1980	Delos Reyes (1995)	Lagoon-Bay	28.5	23,200	179
46	Morocco—marine coast	Stanford et al. (2001)	Coast–Shelf	19.4	19,747	252
47	North Sea	Christensen et al. (2002)	Coast–Shelf	9.9	14,452	276
48	Philippines—San Miguel Bay	Bundy (1997)	Lagoon-Bay	28.5	2,524	30
49	Scotland—west coast (ICES Via)	Morissette and Pitcher (2005)	Coast–Shelf	10.9	4,288	84
50	USA—South Atlantic continental shelf	Okey and Pugliese (2001)	Coast–Shelf	25.0	13,691	406
51	USA—Mid-Atlantic bight	Okey (2001)	Coast–Shelf	15.4	30,581	371
52	USA Alaska, PWS	Okey and Pauly (1999)	Lagoon-Bay	8.0	12,677	451
53	USA West Florida Shelf	Okey and Mahmoudi (2002)	Coast–Shelf	25.3	42,656	718
54	West coast of Vancouver Island	Martell (2000)	Coast–Shelf	11.2		
55	Western Gulf of Mexico—Coast	Arreguin-Sanchez et al. (1993)	Coast–Shelf	25.2	28,971	547

The first model Eq. (4) is highly significant and explains 37% of the total variance. In low temperatures, the mean P/B ratio is roughly equal to 0.7 TL year^{-1} for the fishes with the lowest TLs and decreases toward 0.2 TL year^{-1} for top predators, while in warm temperatures the mean P/B decreases from almost 3.0 to around 0.6 TL year^{-1} (Fig. 3, top). For the Ecopath dataset Eq. (5), the P/B model explains 54% of the total variance. Mean P/B ratios are between 20 and 60 TL year^{-1} for primary produc-

Table 2 – Statistical characteristics of models fitted to the FishBase and the Ecopath datasets: equations tested and explained variance (in bold, selected models)

Dataset	Explicative parameters	n	Model equation	R^2	R^2 adj
FishBase unexploited stocks	θ	162	$P/B = a\exp(c\theta)$	0.259	0.250
	τ	162	$P/B = a\tau^{-b}$	0.121	0.110
		162	$P/B = a\exp(-b\tau)$	0.121	0.110
	τ, θ	161	$P/B = a\tau^{-b}\theta^c$	0.313	0.300
		161	$P/B = a\exp(-b\tau)\theta^c$	0.314	0.301
		162	**$P/B = a\tau^{-b}\exp(c\theta)$**	**0.365**	**0.353**
		162	$P/B = a\exp(-b\tau + c\theta)$	0.366	0.354
FishBase and Pauly's M	τ, θ	5258	$P/B = a\tau^{-b}\exp(c\theta)$	0.443	0.443
		5258	$P/B = a\tau^{-b}\theta^c$	0.415	0.415
Ecopath groups	τ	1718	$P/B = a\tau^{-b}$	0.498	0.498
		1718	$P/B = a\exp(-b\tau)$	0.475	0.475
	τ, θ	**1718**	**$P/B = a\tau^{-b}\exp(c\theta)$**	**0.538**	**0.538**
		1718	$P/B = a\exp(-b\tau + c\theta)$	0.515	0.515

ers and decrease to 0.1–0.3 TL year^{-1} for top predators groups (Fig. 3 bottom). In both cases, P/B values vary approximately by a factor of 3 between cold and warm waters (i.e., between 5 and 25 °C, respectively).

3.2. Residuals and sensitivity analysis

For both models, properties of variances independence and homoscedasticity are respected and residuals appear lognormally distributed (Fig. 4a and e). No relationship is observed between residuals and water temperature, indicating that this effect seems to be properly captured by the model (Fig. 4b and f). Regarding the fitting to fish data, residuals are slightly but significantly lower than zero for P/B ratios based on an age-structured catch curve analysis, while they are higher than zero for data based on a length-converted catch curve analysis (Fig. 4c). This suggests that length-based methods, as opposed to age-based methods, tend to overestimate the natural mortality M. Conversely, no significant effect of the method used for estimating TL is observed (Fig. 4d).

Regarding the fitting to the Ecopath dataset, the P/B model fits well to a large majority of the underlying case studies (Fig. 4g). Nevertheless, significant non-nil residuals are observed for 14 ecosystems, what may relate either to particular flow kinetics or to bad estimates of the P/B ratios in the underlying Ecopath model. No evidence reinforces the second explanation; notably, no relationships were found between mean residuals and the pedigree index of each model ($n = 24$; $R^2 = 0.12$; $P = 0.10$). Conversely, two kinds of factors can explain particular kinetics in some ecosystems. First and not surprisingly, significant non-zero residuals are observed in upwelling ecosystems, which appear characterized by fast trophic transfers, and in coral reef ecosystems that oppositely exhibit slow transfers (Fig. 4h); open sea, coastal or lagoon ecosystems do not differ significantly from the mean P/B model. Second, a significant size effect is observed, with positive residuals and therefore fast transfers in ecosystems whose total biomass is low, while high biomass corresponds to negative residuals and to transfers slower than the mean (Fig. 4i). The same effect can be observed based on the total system throughput TST (not

shown), indicating that ecosystems characterized by high flow and thus a high maturity exhibit less rapid trophic transfers. Reciprocally, transfers were found to be faster in immature ecosystems characterized by high productivity (measured by the total primary production) and moderate TSTs.

Additionally, it is observed that residuals, and therefore flow kinetics, differ between zoological groups (Fig. 4j). The general P/B model applies and mean residuals are close to zero for primary producers, molluscs, crustaceans and fishes, while significant non-zero residuals are obtained for the other groups. Quite logically, this indicates transfers faster than
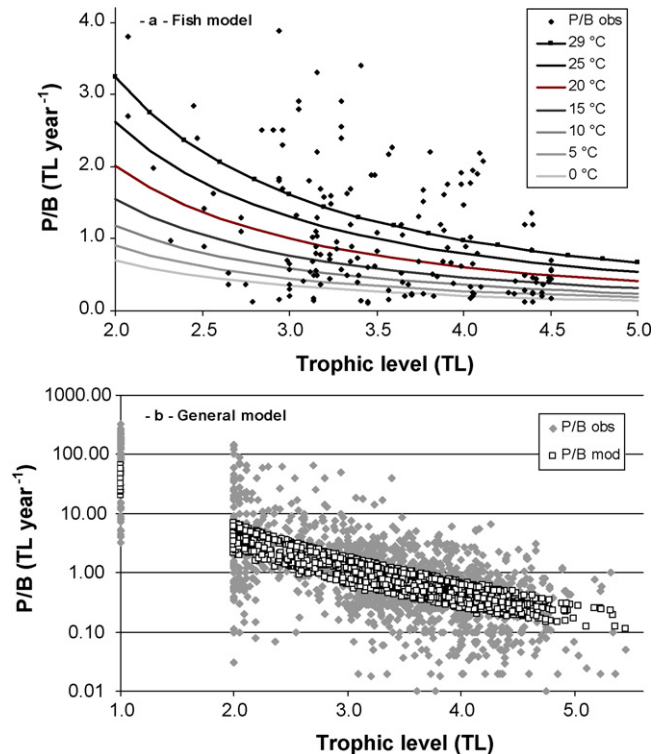

Fig. 3 – P/B model fitted: (a) on the Fishbase dataset ($n = 162$; $R^2 = 0.37$); (b) on the Ecopath dataset ($n = 1718$; $R^2 = 0.54$).
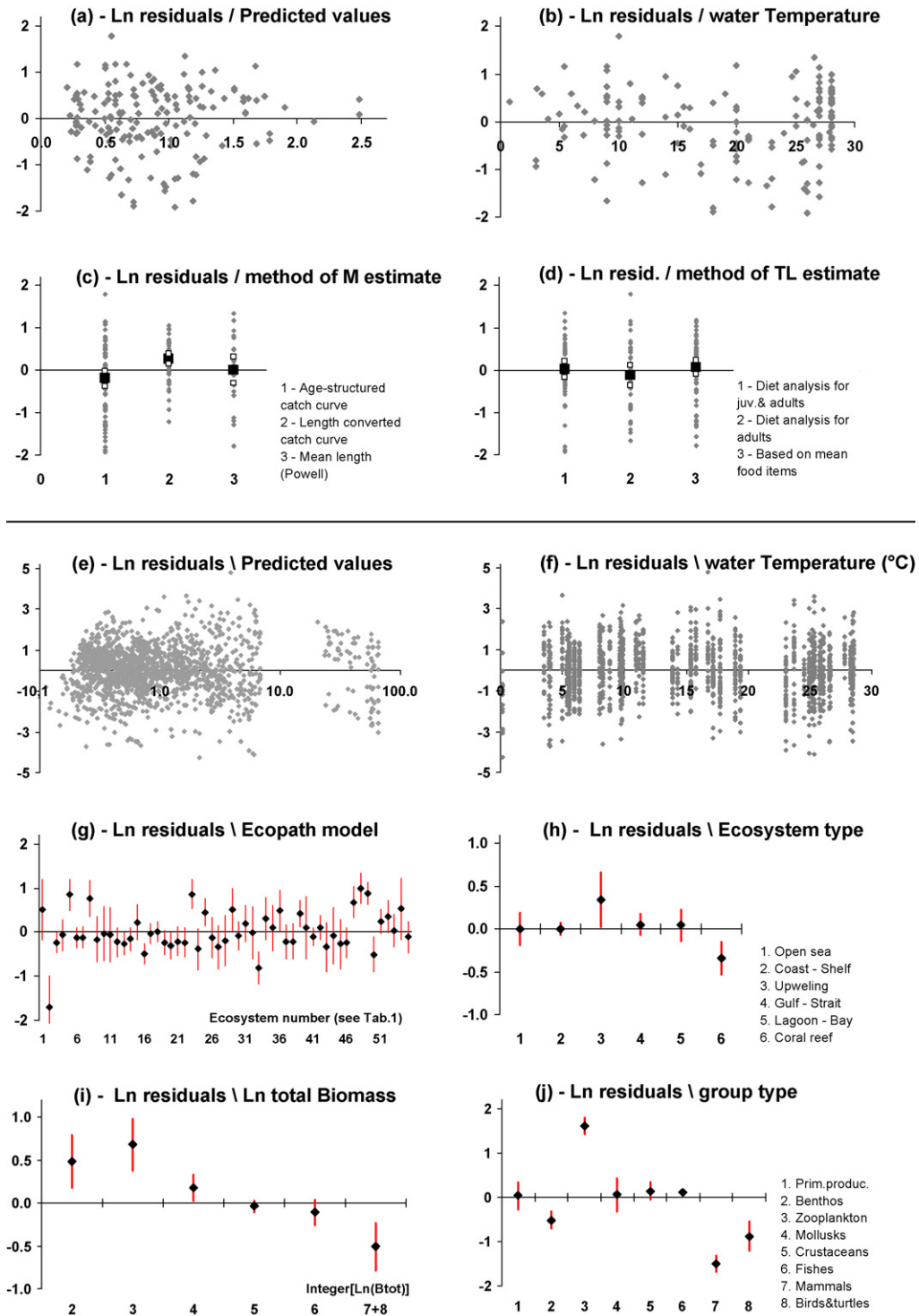
Fig. 4 – Residuals of the P/B models fitted to the FishBase dataset (a–d) and to the Ecopath dataset (e–j) according to various factors; squares in c, d and vertical lines in g–j refer to the confidence limits of the mean residuals.

mean for zooplankton organisms and slower for benthos, marine mammals and birds. The last two groups may be over-represented in Ecopath models; thus, we also verified that the P/B model adjusted with or without them are very similar (Fig. 5a).

Because the datasets are distinct and relate to various ecological groups (fish versus all marine groups), the two models differ, especially in the τ exponent ($b = 1.72$ and 3.26, respectively). Nevertheless, restricting the Ecopath dataset to fish groups changes the model ($b = 2.05$), and leads to results very similar to those obtained with the FishBase dataset (Fig. 5b). The main change occurs for low-trophic levels (between 2 and 3) where fish obviously exhibit slower transfer than organisms such as zooplankton or crustaceans. The P/B model is also con-
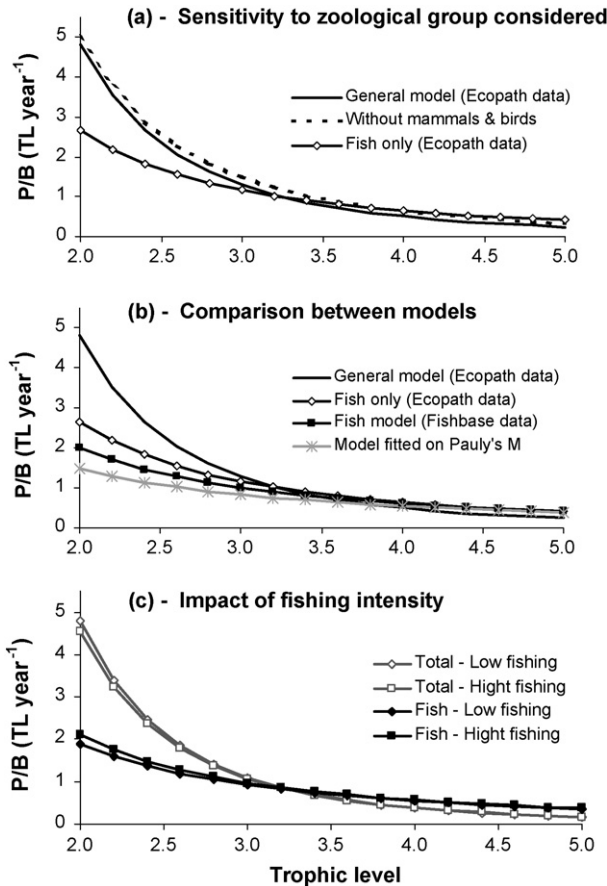
Fig. 5 – Sensitivity of the P/B model to various parameters (conventionally, curves are drawn for a temperature equal to 20 °C).

Table 3 – Statistical characteristics of models including growth parameters: explained variances and significance levels (P)

Independent variables	Explained variance (%)	P level
$a\tau^{-b}\exp(c\theta)K^d$		
K	63.1	0.000
θ	2.4	0.003
τ	2.0	0.002
Total	67.5	0.000
$a\tau^{b}\exp(c\theta)L_\infty^d$		
L_∞	29.6	0.000
θ	17.5	0.000
τ	1.0	0.154

Fig. 6 – Observed and predicted values of P/B, for the model defined by Eq. (6).

sistent with results based on Pauly's empirical equation, even if for a given trophic level the Ecopath data regarding fish lead to slightly higher estimates of P/B than the FishBase data and notably data coming from Pauly's equation. Such differences may be related to the fact that Ecopath P/B values refer to the total mortality Z, while FishBase data refer to natural mortality M of unexploited stocks and estimates obtained from Pauly's equation to M of various stocks.

Finally, the sensitivity of the P/B model to exploitation patterns, for all groups or restricted to fish, appears to be very small (Fig. 5c). This, however, does not prove that fishing has no effect on flow kinetics. It may be the result of a non-integration or an underestimate of such an effect in the underlying Ecopath models themselves.

3.3. Models with growth parameters

Models using the von Bertalanffy growth parameters L_∞ and K as independent variables can be fitted to the FishBase dataset (Tables 3 and 4). Not surprisingly, asymptotic length and trophic level are correlated ($R^2 = 0.29$, based on a power function) and L_∞ explains a higher part of the variance of P/B ratios, than τ. Thus, when L_∞ is used in the model, τ has no additional significant effect (see Table 3). However, a model explaining an even bigger part of the variance of P/Bs can be

built, using the growth coefficient K instead of L_∞. The model is expressed as follows:

$$P/B = 2.56\tau^{-0.78}K^{0.70}\exp(0.020\theta) \tag{6}$$

It explains almost 68% of the total variance observed in the FishBase dataset. The main part of this explained variance is due to the growth coefficient K, which thus appears to be a major factor determining the speed of trophic flow. However, water temperature and trophic level both have a significant additional effect. In other words, variance explained by these two effects is partly, but not totally, already captured by the growth coefficient. Such a model might have a high predictive potential when trophic level, water temperature and growth parameters are known (Fig. 6). More parsimonious models using only K, or K and θ as explicative variables, can be deduced from Table 4, including the very simple linear relationship P/B = 1.89K.

Table 4 – Coefficient values for the model $P/B = a\tau^{-b}\exp(c\theta)K^d$ (values between parentheses have been fixed)

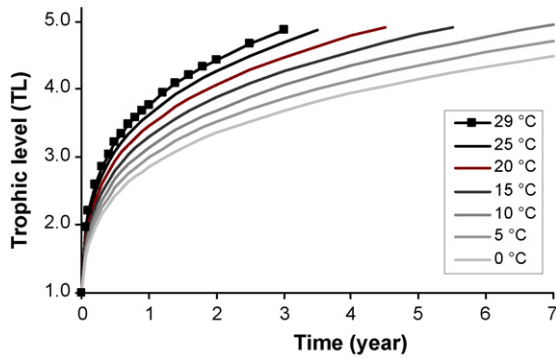| Independent variables	a	b	c	d	R^2
K*	1.89	(0)	(0)	(1)	0.631
K	1.69	(0)	(0)	0.84	0.631
K, τ	3.55	−0.66	(0)	0.80	0.646
K, θ	1.06	(0)	0.018	0.75	0.655
K, θ, τ	2.56	0.78	0.020	0.70	0.675

Fig. 7 – Kinetics of the trophic flow: relationship between time and trophic level, according to the water temperature. The time may be interpreted as the mean age of the biomass.

3.4. Estimates of the mean age of the biomass

Eqs. (3) and (5) define a relationship between the speed of the trophic flow and the trophic level, with the following expression:

$$\frac{\mathrm{d}\tau}{\mathrm{d}t} = a\tau^{-b}$$

This corresponds to the differential equation:

$$\mathrm{d}t = \frac{1}{a}\tau^{b}\,\mathrm{d}\tau$$

Integration leads to an explicit relationship between the time t and the trophic level τ:

$$t = \frac{1}{a(b+1)}[\tau^{b+1} - 1] \tag{7}$$

where t is the mean time required by a unit of biomass to go from trophic level 1 (primary producers) to trophic level τ. The parameter t may also be interpreted as the mean age of biomass present at trophic level τ.

If Eq. (7) is inverted we obtain:

$$\tau = [1 + a(b+1)t]^{1/b+1}$$

where τ is the mean trophic level reached at time t. Based on parameters of Eq. (5), we have:

$$\tau = [1 + 85.97 \ \exp(0.041\theta)t]^{0.235} \tag{8}$$

This expression is the empirical estimate of the theoretical schema presented in Fig. 1. It characterizes the kinetics of the trophic flows at different water temperatures (Fig. 7). For instance, it indicates that the mean age of the biomass present at trophic level 4 is equal to 1.5 years in warm waters, and 3.5 years in cold water (i.e., 25 and 5 °C, respectively). Or, put differently: in 2 years, the biomass entering the food web at trophic level 1 reaches trophic level 3.5 in cold waters, and level 4.3 in warm waters. For intermediate temperatures, the biomass reaches level 2 after around 1 month, level 3 after 6 months, and level 4 after 2.5 years.

4. Discussion

4.1. Regarding P/B as a measure of the trophic flow kinetic

Considering the P/B ratio a measure of the speed of the flow provides a new way to look at this parameter, but in fact it is not a surprising result. Indeed, P/B is a rate of regeneration of the biomass; it relates to the proportion of tissue which is elaborated (whether it survives or not) over a unit of time (Christensen et al., 2005). Each animal or group can be regarded as a 'unit' which transfers the biomass of prey into biomass of a predator, on average from TL = τ to TL = τ + 1. And logically the regeneration rate defines the speed at which the production crosses through a given organism or a given trophic level. Assuming equilibrium, the P/B ratio is equal to the total mortality rate Z (Allen, 1971). This means that the total mortality rate Z, which may be considered a measure of the biomass turn-over (Paloheimo and Dickie, 1970), is also a measure of the speed of the trophic flow, passing through a given trophic level in steady-state conditions.

When a fishery develops, inducing an increasing trend in fishing mortality F, equilibrium can be maintained if the productivity P/B increases. This may be the result of density-dependant regulations, increasing exploitation rates leading to a biomass reduction and thus to reduced competition between individuals. Also, old individuals tend to disappear, leaving the various populations dominated by younger individuals. Finally, this results in a higher biological productivity (see also Ricker, 1975). At the same time, the speed of the trophic flow increases, because tissue regeneration increases and because a higher part of the production leaves the considered trophic level (whether all this production is transferred to the higher TLs or not, due to fishing). Such a process of increasing trophic kinetics with F has been observed in actual case studies (e.g., Jennings and Blanchard, 2004), but was not clearly highlighted when we fitted the P/B model on data characterized by different fishing pressures (Fig. 5c). This may be due to the fact that the process itself was not properly captured in the underlying Ecopath models. Aydin (2004) already noted that density-dependant regulations, which are the basis, for instance, of single species surplus production models, may be underestimated using the EwE model.

Another process that affects the speed of the trophic flow may contribute to maintaining equilibrium when fishing pressure increases. Indeed, the P/B ratio also depends on the natural mortality M, including the predation mortality M_2. Thus, quite logically, the speed of the flow depends on predation mortalities. This means that an increase in the predators' abundance should induce an increase in the predation mortalities, and therefore in the speed of the trophic flow. Conversely, a release in predation may induce slower transfers and thus an accumulation of prey biomass, leading to a compensation effect in term of total biomass. Therefore, changes in the flow kinetics should contribute to top-down regulations.

Finally, M and Z mortalities, P/B ratios, and the speed of the trophic flow dτ/dt are all different ways to look at the same kinetics process, i.e., that by which biomass dies and is regenerated, at the same time it moves through the food

web. These processes are known as being more intensive at the first levels of the food web as well as in warmer waters. Allometric studies have shown that the P/B ratio of organisms is related to their body size or weight (Platt, 1985; Banse and Mosher, 1980; Peters, 1983), to the zoological group or trophic level (Dickie et al., 1987), and to the water temperature (Paloheimo and Dickie, 1966). More recently, general models considering the various zoological groups of the whole animal kingdom were built, linking the metabolism rate of populations to their body weight and body temperature (West et al., 1997; Gillooly et al., 2001; Ernest et al., 2003). At the same time, correlation between the body size and the trophic level was shown at the community level (Jennings et al., 2001). Thus, finding a strong relationship between P/B ratios and the trophic level and the environmental temperature is not surprising for cold-blooded animals. More generally, body size and weight are easy to measure and are pertinent parameters for the scaling of metabolism or productivity of organisms. But reliable trophic level estimates become more and more available, and this new metric can generate a reinterpretation of many empirical relationships between ecological parameters. Using the key metric of the trophic process itself eventually presents a complementary approach to size-based models and a promising avenue for research.

4.2. An empirical estimate of the P/B model

Like all empirical models, the one we propose expressing P/B as a function of the TL and the mean water temperature may be debated. Obviously, the two datasets we used include uncertainty regarding values of the required parameters, because all of them are difficult to estimate (including the mean temperature of an ecosystem). More generally, another dataset would have led to other estimates. Thus, the general shape of the P/B model is more important than the exact values of the parameters of the model equation. From this point of view, the fact that we obtained the same kind of trends based on two independent datasets confirms that this shape relates to a robust ecological pattern. Additionally, we can note that the use of a power function implies that $\ln(TL)$ has a linear effect on $\ln(P/B)$, which indicates that TL should be regarded as a log scale; this seems to be consistent with energetic considerations, energy flow generally decreasing linearly with $\ln(TL)$. As for temperature, we observed that the flow kinetic appears to be directly proportional to $\exp(\theta)$, which corresponds to a linear effect of θ (without log re-scaling) on $\ln(P/B)$ and is similar to what is commonly observed in chemical reactions (e.g., in the Van't Hoff model cited in Regier et al., 1990).

Convergence between both models, the one based on the FishBase dataset and the one based on the Ecopath dataset restricted to fishes, has to be underlined. In the case of the FishBase dataset, we used only 'observed P/B' which are really deduced from field observations (age or length distributions). Even if uncertainty exists for TL or M estimates, our results clearly demonstrated significant relationships between P/B, TL and θ. They also confirmed that results obtained with the Ecopath dataset (and thus Ecopath values themselves) are of the right order. On the other hand, fitting the P/B model to Ecopath data is the only practical way to build a model of flow kinetics which covers all the food web, which is what we were looking for. In this case, 'observed' P/B values have the advantage of being validated for their 'ecological reliability', in the sense that they are fine-tuned to and have to fit all the trophic interactions of the food web. Nevertheless, these values are usually not actually observed (i.e., based on field measurements) but are more often deduced from empirical functions. This may introduce some circularity in the reasoning, and certainly the fitting of an empirical P/B model to 'empirical' P/B ratios can be methodologically controversial. Therefore, the model we obtained here has no proof value of the TL or temperature effects. But in fact, this is not its real purpose. It should rather be interpreted as being a general reformulation, which makes the synthesis between various empirical functions used in Ecopath models and observed values. It thus provides a theoretical estimate, for a mean ecosystem characterized only by its mean water temperature.

Of course, a high variability, depending on species composition and habitat characteristics, exists in practice around this theoretical diagram. From this point of view, results regarding this variability between ecosystems also seem very consistent. The size effect we observed implies that large biomasses (B) are related to slow transfers (P/B), suggesting that the constant process might be biomass flow ($P/\Delta\tau$), while changes in flow kinetics result in changes in abundance. More specifically, one could have anticipated that upwelling ecosystems, characterized by a high primary production and a large biomass of zooplankton, would exhibit fast turn-over and thus a rapid kinetics of trophic flow. Reciprocally, ecosystems dominated by benthic organisms and/or presenting a high proportion of herbivorous fish (such as in coral reefs) should exhibit slower trophic transfers and a smaller number of trophic levels. It would probably be useful to build various models to represent the different types of ecosystems. In the same way, different relationships might be specified for the various zoological groups, as was proposed in the case of body weight models (Ernest et al., 2003). But this requires a larger dataset than we had. Using a 'mean model' is a first step, while keeping in mind that it can underestimate P/B for some ecosystems (upwelling, low biomasses) or zoological groups (zooplankton), and overestimate P/B for others (coral reef ecosystems, benthos, marine mammals).

The particular P/B model we obtained based on TL and growth coefficient K Eq. (6) constitutes what may be seen as a happy by-product of the present study. Once more, empirical expression appears coherent with theoretical considerations. Indeed, it is not surprising to observe a significant relationship between the speed of the trophic flow and the growth rate coefficient. The faster the animal growth is, the more rapid the turn-over. Unlike Pauly's equation, L_∞ has no significant additional effect when K is already taken into account in the model. The most parsimonious model ($M = 1.89K$) indicates that K may even be seen as a rough surrogate of M or P/B. More generally, because the variance explained by models including K is very high, they may be useful additional empirical relationships in order to estimate P/B of fishes (using coefficients of Table 4). We can also notice that the reciprocal of Eq. (6) introduces an expression of TL as a function of M, θ and K. That refers to the idea that under equilibrium conditions, a fish can exhibit a given growth coefficient only if it has a given diet, related to a given TL.

Finally, field measures of production P and biomass B remain of course the best way to parameterise ecosystem models such as Ecopath or EcoTroph. In the absence of such data, it should be recommended to estimate P/B for each ecological group, characterized by a given species composition. Of course, this can be done using empirical equations, including Eq. (6) for fish. As a result, real P/Bs expressed as a function of TL may in a given ecosystem exhibit a complex pattern, not necessarily following a monotonous decreasing curve. As for the P/B model we proposed Eq. (5), it can be considered as the mean curve estimated on average between various ecosystems. It may be useful when using a trophic level-based approach which does not take into account particular ecological groups, as is the case in EcoTroph (Gascuel, 2005; Gascuel and Pauly, in press). But the main interest of the P/B model is probably more theoretical; it may help us to better understand ecosystems' functioning.

4.3. A step toward a general theory of ecosystem functioning?

In many models applied to marine case studies, the ecosystem functioning is more or less reduced to the trophic flow which occurs through the food web (e.g., Pahl-Wostl, 1997; Cury et al., 2003; Christensen and Pauly, 2004). Solar energy and detritus recycling determines the input of biomass at trophic level 1; then, following the pioneered approach of trophic pyramids (Elton, 1927; Lindeman, 1942), the trophic flow is considered the main process which determines the ecosystem state and especially the distribution of biomass between ecological groups or trophic levels, and the ecosystem dynamics over time. Ecopath was probably the first ecosystem model that relied on an explicit representation of these trophic flows between ecosystem compartments. The first model (Polovina, 1984) has been greatly improved upon, especially with the dynamic extension Ecosim (Walters et al., 1997) but the model still relies on a representation of trophic flows between ecological boxes. The EcoTroph model (Gascuel, 2005), where only trophic classes rather than species or groups are considered, may be regarded as the ultimate or caricatured stage of such an approach. Of course, complementary approaches remain necessary, notably the ones more related to biodiversity or to habitat effects. Nevertheless, trophodynamic models have been found to be a very useful way to analyse marine ecosystems' functioning and fishing impact at the ecosystem scale. The fact that such models are mainly applied to marine ecosystems is likely related to the relative homogeneity of many marine habitats and even more to the complexity and the strength of trophic relationships in aquatic ecosystems.

This does not mean that trophic levels are easy to estimate on the field. Because diets are variable and often opportunistic, more work is still needed to estimate not only mean trophic levels but also their standard deviation and their possible changes over time or space. Isotopic and gut contents analyses thus appear to be a key stone step for implementing marine ecosystem modelling and ecosystem approach to fisheries. However, estimate should not be confused with the concept itself (i.e., even if difficult to measure, TL exists as state variable of each biomass unit, according to its food) and developing trophic level-based models constitutes a useful step forward in theoretical context, as well as for specific case studies.

From this perspective of trophodynamic approaches, the speed of the trophic flow (in TL year^{-1}) appears as a key parameter of ecosystem functioning. It is the link that determines the conversion of biomass flow (usually expressed in t year^{-1}, but more rigorously in t TL year^{-1} in the context of a continuous trophic metric) into biomass present at a given trophic level (in tons). For a given flow occurring at a given trophic level, fast transfers lead to low biomasses, because the flow just passes through trophic classes, while slow transfers imply higher biomass due to a process of biomass accumulation in each trophic class. Thus, the biomass flow is always a decreasing function of TL, due to losses occurring during trophic transfers. Conversely, the biomass may exhibit non-monotonous distribution, with higher abundances for less predated groups characterized by slow transfers. This notably explains the "inverted pyramids of biomass" observed in some ecosystems (Odum, 1959).

The speed of the trophic flow is also a factor that partly determines the ecosystem's response to natural or human disturbances, especially fishing. Zoological groups or trophic levels or ecosystems as a whole characterized by fast transfers and thus by fast regeneration capacities would exhibit a higher resilience. This is the case for most of the low trophic level species, which are usually characterized by a high productivity, a fast turn-over and a high resilience. Exceptions exist such as many herbivorous fishes, whose P/B ratio is low and does not follow the rule. Conversely, top predators generally exhibit slow turn-over and are the most vulnerable to fishing. Such general rules remain globally true at the ecosystems level. Immature ecosystems (sensus Odum, 1969) are usually dominated by lower trophic levels and characterized by a high productivity, but a relatively small total biomass and TST (Kay et al., 1989; Christensen, 1995) (due to very high primary production, upwelling ecosystems are exceptions of immature ecosystems where total biomass and TST may be high).

Such immature ecosystems are less complex, and generally less stable than more mature ecosystems (Odum, 1959); as well, their trophic transfers, which pass through simple food chains, are very fast. In other words, intense, simple and fast trophic transfers may be seen as an adaptation to unstable conditions. This, combined with a rapid return to previous conditions following perturbations, enable these ecosystems to exhibit a high resilience to fishing, with catches being compensated for by increased productivity. Additionally the rate of species turn-over is also high for lower organisms (Schoener, 1983) contributing to rapid adaptations. On the other hand, mature ecosystems are more complex and tend to have higher biomass or TST, and slower trophic transfers. Stability is usually high, but productivity low, notably because of strong competition between species or groups. Indeed, complex food webs and low trophic efficiencies may be the way to ensure these ecosystems their high biomass and diversity. This leads to more vulnerable ecosystems, strong perturbations undermining the maintenance of such high biomass and maturity (see also Gunderson and Holling, 2001). Thus, there is evidence of fisheries strongly impacting on such ecosystems, notably by reducing their maturity (e.g., Arreguin-Sanchez et al., 2002; Coll et al., 2006).

In the previous version of the EcoTroph model, it was considered that the speed of the flow had never been estimated before; thus, concluding that P/B ratios can be considered a practical measure of this speed is of course a clear improvement of the trophic level-based approach. Compared to the present estimates, the arbitrary values which had been assumed for kinetics (Gascuel, 2005) were wrong regarding their absolute values (we estimated that trophic level 4 may be reached after 6 months, while the true value appears closer to 2 or 3 years). Nevertheless, the anticipated pattern was perfectly correct with transfers that are faster at low TL. As a consequence, the theoretical results of the EcoTroph model remain unchanged, especially regarding biomass and catch simulation for various exploitation patterns. In addition, knowing the P/B model will allow us to efficiently apply the EcoTroph approach, and its reverse form the Catch Trophic Spectrum Analysis, for the analysis of specific case studies; first attempts seem very promising (Gascuel and Chassot, 2008; Gascuel and Pauly, in press).

5. Conclusion

The key point of this paper is to establish a first knowledge and a quantitative model of the trophic flow kinetics in marine ecosystems. Knowing the general patterns of the speed of the biomass flow according to trophic level helps us to better understand relationships between biomass and production, to analyse and simulate biomass distribution in the food web, and to improve models expressing catch and biomass according to various exploitation patterns and/or functional hypotheses. More generally, this improves our understanding of processes that determine the properties and dynamics of marine ecosystems, and especially their productivity and resilience in face of the current worldwide increase of fisheries. As stated by Brown and Gillooly (2003), using new kinds of data such as trophic levels and modelling ecological phenomena with equations close to physical or chemical processes should eventually contribute to the conceptual unification of ecological theories.

Acknowledgements

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