

A simplified formulation for fish production

G. Mertz and R.A. Myers

Abstract: A new formulation for fish production is presented, one that clearly embodies the balance between aggregate somatic growth and losses due to natural and fishing mortality. The method permits simplified calculation of production over biomass and yield over production ratios; estimates of the latter can be used to investigate the reliability of yield as a proxy for production. Simple applications of the formulation indicate taxonomic variation in the yield to production ratio. Specifically, production is well approximated by yield for many piscivorous species, but yield seriously underestimates production for prey species.

Résumé : Nous présentons une nouvelle formule d'évaluation de la production de poissons qui met clairement en jeu l'équilibre entre la croissance somatique totale et les pertes dues à la mortalité naturelle et à la mortalité par pêche. Il s'agit d'une méthode simplifiée qui permet de calculer les rapports production-biomasse et rendement-production. Cette dernière valeur peut servir à évaluer la fiabilité du rendement comme indicateur de la production. D'après des applications simples de notre formule, le rapport rendement-production comporte une variation taxonomique. Plus précisément, le rendement est un bon indicateur de la production pour bon nombre d'espèces piscivores, mais, dans le cas des espèces-proies, cet indicateur donne une sous-estimation de la production.

[Traduit par la Rédaction]

Introduction

The production of a population of fish, or other aquatic animals, is often sought as a means of establishing an upper limit to the annual harvest (e.g., Ricker 1975; Downing et al. 1990). Equally, the production estimate serves the ecosystems investigator in providing an entry for energy budget models (e.g., Pauly and Christensen 1995; Pauly 1996). In this paper, we present a formulation that simplifies and clarifies the calculation of fish production. In this formulation, fish production through growth is explicitly balanced with losses resulting from natural and fishing mortality.

The developed method is applied to provide a simple formula for the production over biomass ratio, as well as the yield over production ratio. The yield over production ratio directly bears on the validity of using yield to approximate production.

Formulation

For the context described in the introduction, that of harvest limits or energy budgets, it is the long-term time average (sometimes termed equilibrium) production that is sought. The underlying reasoning is clear: a harvest limit is generally envisaged as a time-invariant quantity; energy flows are almost never sufficiently well known that they can be budgeted on a time-dependent basis. Accordingly, the emphasis here is on obtaining estimates of the time-averaged production.

Clarke (1946) defined fish production as the "amount of

tissue elaborated per unit time per unit area, regardless of its fate." This definition is embodied in the formulations used in the germinal studies of this topic, such as Ricker (1946) and Allen (1950, 1971) (note, however, that Allen dealt principally with the tissue developed in some time interval, rather than with an instantaneous rate). For each fish, the rate of elaboration of tissue is simply dw_i/dt , where w_i is the mass of the specified fish (fish i). The total production (P) for the population is thus

$$(1) \quad P = \sum_i dw_i / dt.$$

The sum is taken over all fish in the given area. Typical units for production are kilograms per hectare per year.

The fish can be aggregated into age categories, with N_a fish at age a , so that the total number of fish is the sum of N_a over all ages present (N_a will generally be in numbers per unit area). Equation 1 becomes

$$(2) \quad P = \sum_{a=0}^{a=a_m} N_a (dw / dt)_a$$

where a_m is the maximum age in the population. In eq. 2, we are in effect summing over $a_m + 1$ cohorts, with the production in each cohort being given by $N_a(dw/dt)_a$. It can be shown (see Appendix 1) that eq. 2 is equivalent to the often-cited Allen method.

The age categories in eq. 2 need not be 1 year wide but can be made as narrow as desired. This will allow us to replace the sum with a more tractable integral. When a is treated as a continuous variable, the growth rate becomes $dw(a)/da$ and N_a is replaced with $n(a)da$ where $n(a)$ is the number (in a unit area) per unit age. (The total number of fish, per unit area, is given by $\int_0^{a_m} n(a)da$.) Equation 2 can now be written as

$$(3) \quad P = \int_0^{a_m} n(a) \frac{dw(a)}{da} da.$$

Received November 27, 1996. Accepted June 17, 1997.
J13771

G. Mertz. Department of Fisheries and Oceans, Northwest Atlantic Fisheries Centre, P.O. Box 5667, St. John's, NF A1C 5X1, Canada.

R.A. Myers.¹ Killam Chair in Ocean Studies, Department of Biology, Dalhousie University, Halifax, NS B3H 4J1, Canada.

¹ Author to whom all correspondence should be addressed.
e-mail: Ransom.Meyers@Dal.Ca

The production, as given by eq. 3, will have units of mass per unit time per unit area.

Equations 1, 2, and 3 can be used to calculate production as a function of time, that is, time-dependent numbers-at-age and growth-at-age can be accommodated in these equations. Ideally, the time-averaged production would be obtained by calculating a time series for production and then averaging. In practice, this is generally not feasible, and the time-averaged production must be estimated from time-averaged numbers-at-age and growth-at-age. It is clear from eq. 2 or eq. 3 that this will not bias the result, provided that there is no correlation between the time histories of numbers at a given age and growth at that age. The magnitude of the error suffered through neglect of this correlation is dealt with in Appendix 2 where it is concluded that, in general, the error is not severe. It must be noted that there will be individual fish stocks for which the numbers-growth correlation is strong, and for these the effect of the correlation cannot be neglected (Appendix 2 provides a means of making the necessary correction). It must also be remarked that many ecosystems models exploit the advantage of scale by aggregating the production of many stocks into trophic levels, a measure that will attenuate the influence of any particular fish stock for which production is poorly estimated. Henceforth, it should be understood that all quantities are time-averaged.

It is now convenient to introduce the survival function $s(a)$ which gives the ratio of the number (per unit area) of fish at age a , $n(a)da$, to the number (per unit area) of age 0 fish, n_0da ; specifically, $s(a) = n(a)da/(n_0da) = n(a)/n_0$. With the introduction of age-specific natural and fishing mortalities, $M(a)$ and $F(a)$, respectively, we can write the survival function as $s(a) = \exp \int_0^a [-M(a') - F(a')]da'$ (e.g., Gulland 1977, p. 80). Equation 3 can now be expressed as

$$(4) \quad P = n_0 \int_0^{a_m} s(a) \frac{dw(a)}{da} da.$$

Equation 4 can be reexpressed through integration by parts:

$$(5) \quad P = n_0 \left[[s(a)w(a)]_0^{a_m} - \int_0^{a_m} w(a) \frac{ds(a)}{da} da \right].$$

With $s(a)$ as given above, it is easily shown that $ds(a)/da = -[M(a) + F(a)]s(a)$. Thus

$$(6) \quad P = n_0 \left[[s(a)w(a)]_0^{a_m} + \int_0^{a_m} [M(a) + F(a)]s(a)w(a)da \right],$$

an expression that can be further simplified.

The first term, inside the large square brackets in eq. 6, is equal to $s(a_m)w(a_m) - s(0)w(0)$ and may be immediately rewritten as $-s(0)w(0)$ because $s(a_m) = 0$ by definition. Here, age 0 is taken to be the onset of feeding in the larval stage, the phase at which tissue growth commences. The term $s(0)w(0)$ can be compared with the second term inside the large square brackets in eq. 6, which we approximate as $w(a_r)s(a_r) \int_{a_r}^{a_m} (M + F)da$, where a_r is a reference age, perhaps the age-at-maturity (this somewhat underestimates the size of the approximated term). We simplify this to just $w(a_r)s(a_r)$ with the approximation $\int_{a_r}^{a_m} (M + F)da \approx 1$ (this assumes that the spawning lifetime $a_m - a_r$ is roughly equal to $1/(M + F)$, where M and F are the typical mortalities for adult fish). Thus the relative magnitudes of the first and second terms inside the

large square brackets in eq. 6 are just $w(0)s(0)/[w(a_r)s(a_r)]$. The ratio $s(0)/s(a_r)$ will be in the range of 10^3 to 10^5 . Using the data of Pepin (1993) for larval fish, $w(0)/w(a_r) \leq 10^{-8}$ (based on a $w(a_r)$ of 10 g or greater), and thus, $w(0)s(0)/[w(a_r)s(a_r)] \ll 1$. It follows that the first term inside the large square brackets in eq. 6 may be neglected.

Given the considerations above, we can now write eq. 6 as

$$(7) \quad P = \int_0^{a_m} [M(a) + F(a)]W_c(a)da$$

where $W_c(a) = n_0s(a)w(a)$; $W_c(a)da$ is the mass (per unit area) of a cohort of age a . This relationship simply equates the production of biomass to its destruction (by natural and fishing mortality), an equality that must hold if a steady state is to prevail. By introducing the age-specific somatic growth rate, $G(a) \equiv w(a)^{-1}dw(a)/da$ (e.g., Ricker 1975), eqs. 4 and 7 can be combined to yield

$$(8) \quad \int_0^{a_m} [G(a) - (M(a) + F(a))]W_c(a)da = 0.$$

This equation makes explicit the balance between growth and mortality, integrated over the lifetime of a cohort. It is clear from eq. 8 that $G(a) - M(a) - F(a)$ must change sign at some point during the life of the cohort, or be equal to zero for all ages.

Production over biomass

The ratio of production to biomass is often sought by marine ecologists. To obtain biomass (B), which is the total mass (per unit area) of fish extant, one simply "sums" the cohort weights ($W_c(a)da$) over age:

$$(9) \quad B = \int_0^{a_m} W_c(a)da.$$

It is helpful to introduce the biomass-averaged natural mortality, fishing mortality, and growth rate, \tilde{M} , \tilde{F} , \tilde{G} . These are averages over age, weighted according to the contribution of each cohort to the total biomass; specifically:

$$(10) \quad \{\tilde{M}, \tilde{F}, \tilde{G}\} = \frac{\int_0^{a_m} \{M(a), F(a), G(a)\} W_c(a)da}{\int_0^{a_m} W_c(a)da}.$$

With these definitions, from eqs. 9 and 7, we have

$$(11) \quad \frac{P}{B} = \tilde{M} + \tilde{F}.$$

If $M(a) = M$ and $F(a) = F$ (that is, they are constant), then one immediately has $P/B = M + F$, a result given by Dickie (1972). Using eq. 8, one can easily show

$$(12) \quad \tilde{G} = \tilde{M} + \tilde{F} \rightarrow \tilde{G} = \frac{P}{B}.$$

Thus, the P/B ratio is equal to biomass-averaged total mortality (eq. 11) or, equivalently, the biomass-averaged somatic growth rate (eq. 12).

Yield versus production

Yield is generally an important component of production. In some realms, yield alone may suffice to measure production.

We will now provide a simple equation for the ratio of yield to production, which will be applied to fisheries data in the next section.

The yield from a cohort of age a is calculated by multiplying the cohort mass ($W_c(a)da$) by the fishing mortality ($F(a)$). The total yield (Y), in say kilograms per hectare per year, is then calculated by "summing" over all cohorts present:

$$(13) \quad Y = \int_0^{a_m} F(a)W_c(a)da.$$

It is thus easily shown that

$$(14) \quad Y = \tilde{F}B.$$

Hence, from eqs. 11 and 14:

$$(15) \quad \frac{Y}{P} = \frac{\tilde{F}}{\tilde{F} + \tilde{M}}.$$

Equation 15 permits ready estimation of the yield to production ratio.

Applications

Practical calculation of yield over production, etc.

In general, a full set of $M(a)$, $F(a)$ data will not be available, and a working approximation for \tilde{M} , \tilde{F} is desirable. Using data from Pepin (1991, 1993), it is easily shown that the biomass of larvae, for any realistic conditions, is so small that the influence of this stage can be neglected in the calculation of \tilde{M} , \tilde{F} . Assuming constant M , F during the juvenile stage (M_j , F_j) and the mature stage (M_m , F_m), we can write from eq. 10

$$(16) \quad \tilde{M} = (M_j B_j + M_m B_m) / B$$

where B_j , B_m are the biomasses of juvenile and mature fish, respectively, and $B = B_j + B_m$ is again the total biomass. Similarly:

$$(17) \quad \tilde{F} = (F_j B_j + F_m B_m) / B.$$

As we will show below, further simplification of eqs. 16 and 17 is possible.

For lightly fished stocks, the mature biomass is likely to be many times the juvenile biomass, in which case, $\tilde{M} \approx M_m$, $\tilde{F} \approx F_m$. For example, we calculated \tilde{M} for two natural mortality schedules for Pacific hake (*Merluccius productus*), using data from Smith (1995), and found, for both cases, that \tilde{M} and M_m differed by less than 5%. This is strictly a consequence of the preponderant contribution of mature fish to the total biomass.

For heavily fished stocks, the mature biomass may be no larger than the juvenile biomass, in which case, $\tilde{M} \approx (M_j + M_m)/2$ and $\tilde{F} \approx (F_j + F_m)/2$. The juveniles in highly exploited stocks are likely to become heavily fished so that $F_j \approx F_m$ and thus, $\tilde{F} \approx F_m$, the same result that we have suggested for lightly harvested stocks. The juvenile mortality rate for most species is poorly known, but it is safe to assume that it is very similar, late in the juvenile phase, to the adult mortality rate. At the late stage of the juvenile phase the juvenile biomass is at its maximum, and thus the best estimate for M_j may be the mortality rate prevailing in the late stage, specifically, $M_j \approx M_m$. This would yield, from eq. 16, $\tilde{M} \approx M_m$.

Thus, for the purposes of practical calculation, the following approximations will be acceptable in most circumstances:

$$(18) \quad \frac{Y}{P} \approx \frac{F_m}{F_m + M_m}, \quad \frac{P}{B} \approx F_m + M_m.$$

Yield versus production

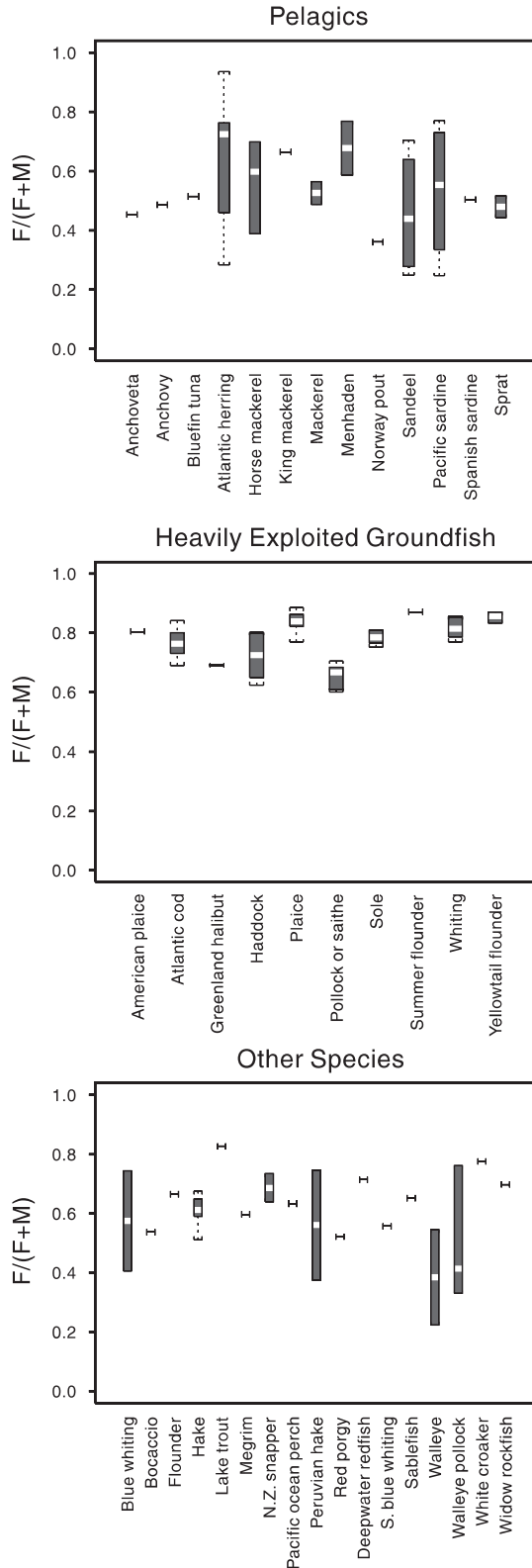
In freshwater domains, yield is often assumed to be a direct substitute for production (e.g., see table 1 of Downing et al. 1990). In marine realms, production is frequently calculated from yield with the application of a provisional adjustment factor. Equation 18 can immediately be applied to determine the relationship between yield and production, for major fish stocks, those for which the M_m and F_m are available. We have compiled, from the data described in Myers et al. (1995) (some data sets will appear in the next release of the database), the M_m and F_m values for about 200 marine and freshwater fish stocks, and we have entered these into eq. 18 to estimate Y/P (the F_m values are time-averaged). Figure 1 presents the species-aggregated Y/P values displayed in box and whisker format. Table 1 gives the pertinent information on a species by species basis.

From Fig. 1, it is evident that species averages of estimated Y/P range from about 0.3 to 0.8. It is apparent that there is some taxonomic variation. Many of the pelagic species such as anchovy, sandeel, and sprat are forage fish, the prey of piscivores, and thus experience high M_m values (Table 1). The high M_m limits the ability of these species to withstand high fishing pressure, and thus, $F_m/(F_m + M_m)$ tends to the low range of values observed. This is confirmed by the work of Patterson (1992), whose data show that a typical $F_m/(F_m + M_m)$ for small pelagics is about 0.5, in agreement with Fig. 1. In contrast, the groundfish species are generally typified by lower M_m values, since these are piscivores (rather than being the prey of many other fish species). Accordingly, these species are better able to endure high fishing mortality, and this, in conjunction with the low M_m values, leads to Y/P estimates that are generally close to 0.8.

Data for freshwater fish were less accessible, but we were able to enter two freshwater species in Fig. 1, lake trout and walleye (genus and species are given in Table 1). The walleye populations are evidently quite lightly exploited, as one might anticipate for recreationally fished stocks. Data were available for only one lake trout stock (Lake Opeongo in Ontario; Shuter et al. 1987) and it shows high exploitation, despite the fact that the fishery is recreational. It is evident that yield can significantly underestimate production for a freshwater species.

From the perspective of trophic modelling of marine ecosystems, the ratio of aggregate fish production to total primary production is of some interest, as it provides a test of the accepted values for the mean number of trophic levels and the transfer efficiency (e.g., Pauly and Christensen 1995; Pauly 1996). Production can be obtained from the known catches if the P/Y ratio is known. As noted by Pauly (1996), a number of studies have assumed that production is about equally divided between predation and catches. Since we have provided P/Y ratios in Fig. 1, this proposed value of 0.5 can be tested, for specified aggregates. For example, the appropriate P/Y for commercial finfish species ranges from about 0.5 to 0.8, and for a global aggregate, a P/Y of about 0.6 would appear to be appropriate, given the dominance of pelagics in world catches.

Fig. 1. Box and whisker plots of yield over production, Y/P , estimated from the approximation $\bar{F}_m/(\bar{F}_m + M)$, for pelagic fish, heavily exploited groundfish in the North Atlantic, and other species (the bar designates a time-average). For the first plot (Pelagics), the species from the genus *Trachurus* were combined under the common name horse mackerel and the species from the genus *Brevoortia* were combined under the name menhaden.



It is evident that the method and data provided here can be used to corroborate and (or) refine assumptions about production versus yield, thereby providing more reliable estimates of global production.

Production prior to exploitation

It may be of ecological interest to acquire estimates of the production of a stock prior to its exploitation. For many fish stocks, there exists a flat region in the stock recruit curve where recruitment is almost independent of standing biomass (although at sufficiently low stock size, recruitment will decline; Myers and Barrowman 1996). In this regime, the biomass is approximately linear in the total mortality, $M_m + F_m$, provided that the total mortality is not large and assuming that the juveniles are not fished (and assuming that density-dependent growth is not significant in this low F_m range). In this situation, $M_m \approx \tilde{M}$ and $M_m + F_m \approx \tilde{M} + \tilde{F}$. Using the linearity of the biomass in total mortality, we now have $B/B_0 \approx \tilde{M}/(\tilde{M} + \tilde{F})$ where B_0 refers to the unfished biomass. From eq. 11, we have $P_0/B_0 = \tilde{M}$ where P_0 refers to the production in the absence of fishing. Combining these latter two equations with eq. 11 shows that $P/P_0 \approx 1$, that is, to a first approximation the fish production is independent of harvest rate, at low F_m values. Thus, for lightly exploited stocks, the extant production is a useable approximation for the virgin production.

Using similar reasoning, we can estimate the maximum feasible ratio of yield to virgin production, P_0 . Since $Y/P_0 = (Y/P)(P/P_0)$, using eq. 15, we have $Y/P_0 = [\tilde{F}/(\tilde{F} + \tilde{M})](P/P_0)$. As above, in the small \tilde{F} , \tilde{M} range, we can set $P/P_0 = 1$ and thus, $Y/P_0 = \tilde{F}/(\tilde{F} + \tilde{M})$. Thus, if $\tilde{F} = \tilde{M}$, $Y/P_0 = 0.5$, that is, it is possible to harvest one half of the virgin production of the stock. If the regime of constant recruitment extends as far as $\tilde{F} = 2\tilde{M}$, then it would be possible to harvest two thirds of the virgin production. These simple calculations suggest that one is unlikely to obtain much more than one half the unfished production.

Turnover time for semelparous species

An interesting case is that of semelparous species, such as Pacific salmon of the genus *Oncorhynchus*. Let us suppose that survival abruptly declines to 0 at a_m (the fish die after reproduction at age a_m). One can easily show for this case that

$$(19) \quad \frac{P}{B} = \tilde{M} + \frac{n_0 w(a_m) s(a_m)}{B}$$

where \tilde{M} is evaluated on the interval 0 to $a_m - \Delta a$ where Δa is some small age increment introduced to ensure that the calculation of \tilde{M} does not include the spike in mortality at $a = a_m$. (Strictly, $s(a_m)$ should read $s(a_m - \Delta a)$.) Because a_m is approximately the age at which $s(a)w(a)$ is maximized (e.g., Roff 1992), the biomass ($B = n_0 \int_0^{a_m} w(a)s(a)da$) can be approximated as follows:

$$(1/2)n_0 w(a_m) s(a_m) a_m \leq B \leq n_0 w(a_m) s(a_m) a_m.$$

Thus, we can write $B = \gamma n_0 w(a_m) s(a_m) a_m$, where γ is a constant ($1/2 \leq \gamma \leq 1$) that can be calculated from the growth and mortality characteristics of the population. Thus, from eq. 19,

$$(20) \quad P/B = \tilde{M} + 1 / (\gamma a_m).$$

If the mortality rate is low, such that $\tilde{M} a_m \ll 1$, then $P/B \approx$

Table 1. Parameters used to approximate production (P) and yield (Y) for commercially exploited marine and freshwater fish species.

	M	Y/P	\bar{F}		M	Y/P	\bar{F}
Clupeiformes	0.37	0.56	0.61	Scombridae	0.16	0.48	0.22
Clupeidae	0.32	0.56	0.59	<i>Scomber scombrus</i> (Atlantic mackerel)	0.18	0.45	0.19
<i>Brevoortia patronus</i> (Gulf menhaden)	1.1	0.57	1.56	<i>Scomberomorus cavalla</i> (king mackerel)	0.17	0.57	0.33
<i>Brevoortia tyrannus</i> (Atlantic menhaden)	0.45	0.75	1.49	<i>Thunnus thynnus</i> (bluefin tuna)	0.14	0.47	0.15
<i>Clupea harengus</i> (Atlantic herring)	0.19	0.59	0.47	Sparidae	0.13	0.52	0.19
<i>Sardina pilchardus</i> (Spanish sardine)	0.33	0.49	0.33	<i>Pagrus auratus</i> (New Zealand snapper)	0.06	0.55	0.14
<i>Sardinella brasiliensis</i> (orangespot sardine)	1.2	0.41	0.87	<i>Pagrus pagrus</i> (red porgy)	0.28	0.47	0.31
<i>Sardinops sagax</i> (Pacific sardine)	0.46	0.52	0.8	Pleuronectiformes	0.14	0.78	0.6
<i>Sprattus sprattus</i> (sprat)	0.33	0.46	0.31	Bothidae	0.2	0.87	1.35
Engraulidae	1	0.46	0.88	<i>Paralichthys dentatus</i> (summer flounder)	0.2	0.87	1.35
<i>Engraulis encrasicolus</i> (anchovy)	0.8	0.47	0.76	Pleuronectidae	0.15	0.8	0.68
<i>Engraulis ringens</i> (Peruvian anchoveta)	1.2	0.44	1	<i>Hippoglossoides platessoides</i> (American plaice)	0.2	0.76	0.83
Gadiformes	0.25	0.68	0.61	<i>Platichthys flesus</i> (flounder)	0.2	0.65	0.4
Gadidae	0.25	0.68	0.61	<i>Pleuronectes ferrugineus</i> (yellowtail flounder)	0.2	0.84	1.18
<i>Gadus morhua</i> (Atlantic cod)	0.2	0.75	0.68	<i>Pleuronectes platessa</i> (plaice)	0.11	0.83	0.59
<i>Melanogrammus aeglefinus</i> (haddock)	0.2	0.71	0.58	<i>Reinhardtius hippoglossoides</i> (Greenland halibut)	0.15	0.67	0.34
<i>Merlangius merlangus</i> (whiting)	0.2	0.81	0.93	Scophthalmidae	0.2	0.6	0.3
<i>Merluccius bilinearis</i> (silver hake)	0.4	0.61	0.68	<i>Lepidorhombus whiffiagonis</i> (megrim)	0.2	0.6	0.3
<i>Merluccius gayi</i> (Peruvian hake)	0.36	0.54	0.57	Soleidae	0.1	0.77	0.37
<i>Merluccius merluccius</i> (hake)	0.2	0.58	0.29	<i>Solea vulgaris</i> (sole)	0.1	0.77	0.37
<i>Micromesistius australis</i> (southern blue whiting)	0.2	0.49	0.25	Salmoniformes	0.11	0.8	0.52
<i>Micromesistius poutassou</i> (blue whiting)	0.2	0.53	0.36	Salmonidae	0.11	0.8	0.52
<i>Pollachius virens</i> (pollock or saithe)	0.2	0.64	0.39	<i>Salvelinus namaycush</i> (lake trout)	0.11	0.8	0.52
<i>Theragra chalcogramma</i> (walleye pollock)	0.31	0.48	0.46	Scorpaeniformes	0.11	0.58	0.21
<i>Trisopterus esmarkii</i> (Norway pout)	1.6	0.35	0.9	Anoplopomatidae	0.1	0.64	0.19
Perciformes	0.28	0.49	0.35	<i>Anoplopoma fimbria</i> (sablefish)	0.1	0.64	0.19
Ammodytidae	0.51	0.44	0.5	Scorpaenidae	0.11	0.57	0.21
<i>Ammodytes marinus</i> (sandeel)	0.51	0.44	0.5	<i>Sebastes alutus</i> (Pacific ocean perch)	0.05	0.53	0.09
Carangidae	0.23	0.54	0.35	<i>Sebastes entomelas</i> (widow rockfish)	0.15	0.66	0.35
<i>Trachurus symmetricus murphyi</i> (South Pacific horse mackerel)	0.4	0.57	0.59	<i>Sebastes mentella</i> (deepwater redfish)	0.1	0.56	0.25
<i>Trachurus trachurus</i> (horse mackerel)	0.15	0.52	0.22	<i>Sebastes paucispinis</i> (bocaccio)	0.15	0.52	0.17
Percidae	0.3	0.37	0.22				
<i>Stizostedion vitreum</i> (walleye)	0.3	0.37	0.22				
Scianidae	0.29	0.77	1.01				
<i>Argyrosomus argentatus</i> (white croaker)	0.29	0.77	1.01				

Note: The ratio of yield over production, Y/P , is estimated from the approximation $\bar{F}_m/(\bar{F}_m + M)$ where the bar designates a time-average.

$1/(\gamma\alpha_m)$. This case provides confirmation of one's intuition that the turnover time (the reciprocal of P/B) for a semelparous species should be approximately equal to its lifetime.

Conclusions

We have presented a formulation for fish production that clearly portrays the source-sink relationship of production and mortality. The method was applied to show that the production over biomass ratio is simply the sum of the biomass-averaged natural and fishing mortalities.

The formulation shows that yield over production is given by the ratio of biomass-averaged fishing mortality to the biomass-averaged total mortality. We have shown that this can be simplified in most cases to the ratio of the adult fishing mortality to the adult total mortality. This simplification permits ready evaluation of the utility of yield as a proxy for production.

We compiled, for a broad range of taxa, the ratios of adult

fishing mortality to adult total mortality. The data revealed interpretable patterns, in that piscivores exhibited mortality ratios around 0.8, while prey species, typified by high natural mortality, had mortality ratios nearer 0.5. Yield can be used as a direct approximation of production for many of the piscivorous species, and the yield of a prey species can be adjusted, using the ratios provided by our analysis, to estimate production.

Acknowledgements

We thank Nick Barrowman and Pierre Pepin for their input. We are grateful to the journal reviewers for their close scrutiny of the manuscript.

References

- Allen, K.R. 1950. The computation of production in fish populations. N.Z. Sci. Rev. 8: 89.

- Allen, K.R. 1971. Relation between production and biomass. *J. Fish. Res. Board Can.* **28**: 1573–1581.
- Chapman, D.W. 1978. Production. *In* Methods for assessment of fish production in fresh waters. *Edited by* T. Bagenal. Handbook No. 3. 3rd ed. Blackwell Scientific Publications, Oxford, U.K. pp. 202–217.
- Clarke, G.L. 1946. Dynamics of production in a marine area. *Ecol. Monogr.* **16**: 321–335.
- Dickie, L.M. 1972. Food chains and fish production. *ICNAF Spec. Publ.* **8**: 201–219.
- Downing, J.A., Plante, C., and Lalonde, S. 1990. Fish production correlated with primary productivity, not the morphoedaphic index. *Can. J. Fish. Aquat. Sci.* **47**: 1929–1936.
- Gulland, J.A. 1977. The analysis of data and development of models. *In* Fish population dynamics. *Edited by* J.A. Gulland. John Wiley & Sons, London, U.K. pp. 67–95.
- Mertz, G., and Myers, R.A. 1995. Estimating the predictability of recruitment. *Fish. Bull.* **93**: 657–665.
- Myers, R.A., and Barrowman, N.J. 1996. Is fish recruitment related to spawner abundance? *Fish. Bull.* **94**: 707–724.
- Myers, R.A., Bridson, J., and Barrowman, N.J. 1995. Summary of worldwide spawner and recruit data. *Can. Tech. Rep. Fish. Aquat. Sci.* No. 2024.
- Patterson, K. 1992. Fisheries for small pelagic species: an empirical approach to management targets. *Rev. Fish. Biol. Fish.* **2**: 321–338.
- Pauly, D. 1996. One hundred million tons of fish, and fisheries research. *Fish. Res.* **25**: 25–38.
- Pauly, D., and Christensen, V. 1995. Primary production required to sustain global fisheries. *Nature (London)*, **374**: 255–257.
- Pepin, P. 1991. Effect of temperature and size on development, mortality, and survival rates of the pelagic early life history stages of marine fish. *Can. J. Fish. Aquat. Sci.* **48**: 503–518.
- Pepin, P. 1993. Application of empirical size-dependent models of larval vital rates to the study of production: accuracy and association with adult stock dynamics in a comparison among species. *Can. J. Fish. Aquat. Sci.* **50**: 53–59.
- Ricker, W.E. 1946. Production and utilization of fish populations. *Ecol. Monogr.* **16**: 373–391.
- Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Board Can.* No. 191.
- Rijnsdorp, A.D. 1994. Population regulating processes during the adult phase in flatfish. *Neth. J. Sea Res.* **32**: 207–223.
- Roff, D.A. 1992. The evolution of life histories: theory and analysis. Chapman and Hall, New York.
- Shuter, B.J., Matuszek, J.E., and Regier, H.A. 1987. Optimal use of creel survey data in assessing population behaviour: Lake Opeongo lake trout (*Savelinus namaycush*) and smallmouth bass (*Micropterus dolomieu*), 1936–83. *Can. J. Fish. Aquat. Sci.* **44**(Suppl. 2): 229–238.
- Smith, P.E. 1995. Development of the population biology of the Pacific hake (*Merluccius productus*). *CALCOFI Rep.* **16**: 144–152.
- Weatherly, A.H., and Gill, H.S. 1987. The biology of fish growth. Academic Press, London, U.K.

Appendix 1

Here, we describe the Allen (1950, 1971) method as presented in detail by Chapman (1978). Note that, in the Allen treatment, the quantity referred to as production is not a rate; we will refer to the quantity defined by Allen as “integrated production”. In this technique, a cohort is tracked as it ages and its integrated production is calculated as a sum over age increments (Δa); we designate the number of increments to be K . (Note that we have translated Chapman’s notation into our own.) The increment of integrated production is given by $(dw/dt)_a N_a \Delta a$; see eq. 1 of Chapman (1978). Thus, the integrated production per cohort (the sum of increments) is $\sum_0^{a_m} (dw/dt)_a N_a \Delta a$.

To obtain the production per cohort from integrated production per cohort, one divides by the lifetime of the cohort,

according to Allen (1971). The lifetime of the cohort is $K\Delta a$ in the example here. Since Δa is generally taken to be the time between births of cohorts (typically 1 year), there are $(K\Delta a)/\Delta a = K$ cohorts present. Thus

$$P = K \times \frac{1}{K\Delta a} \times \sum_0^{a_m} (dw/dt)_a N_a \Delta a = \sum_0^{a_m} (dw/dt)_a N_a$$

That is, we have first divided the integrated production per cohort by the cohort lifetime ($K\Delta a$) and then multiplied by the number of cohorts present (K) to obtain the production. The resulting expression is equivalent to eq. 2.

Appendix 2

Before time-averaging eq. 3, it is convenient to decompose the numbers-at-age and growth-at-age into mean and time-varying components: $n(a) = \bar{n}(a) + n'(a)$; $dw(a)/da = \overline{dw(a)/da} + (dw(a)/da)'$ (overbars indicate time averages and primes denote fluctuations). If we time-average eq. 3, we obtain

$$\bar{P} = \int_0^{a_m} \bar{n}(a) \frac{\overline{dw(a)}}{da} [1 + r(a)CV_n(a)CV_{dw/da}(a)] da$$

where CV denotes the coefficient of variation for the subscripted quantity and $r(a)$ is the correlation coefficient between the time histories of $n(a)$ and $dw(a)/da$.

As noted in the text, production estimates tacitly assume

that the first term in the integral above suffices in the calculation of \bar{P} . This will obviously be true if $r(a)$ is negligible. A nonnegligible $r(a)$ would arise if growth were density dependent or if recruitment (which determines the variability of $n(a)$) and growth were both correlated with a common environmental factor.

We can roughly estimate the maximum plausible size of the term containing $r(a)$. The quantity $CV_n(a)$ is essentially the CV for recruitment, and it will generally be less than 1 (Mertz and Myers 1995). Less information is available to estimate $CV_{dw/da}(a)$, but given that growth curves can generally be fitted without great scatter (e.g., Weatherly and Gill 1987), we specify $CV_{dw/da}(a) < 0.5$. Strong covariation of growth and

numbers would perhaps imply $|r(a)| = 0.7$, surely a strong correlation in this context. Given these estimates, we have $|r(a)CV_n(a)CV_{dw/da}(a)| < 0.35$ (note that density-dependent growth would imply that the sign of this product will be negative). Note that the integral above defining \bar{P} encompasses all ages, while $|r(a)CV_n(a)CV_{dw/da}(a)|$ is likely to be appreciable for at most a narrow range of ages, those for which growth shows significant fluctuations. This suggests that the inequality immediately above overestimates the maximum bias.

Suppose again that recruitment and growth covary because of a common environmental influence. In this situation, $r(a)$ is positive, and in the worst case, production would be underestimated, through neglect of the covariation, by $100\% \times (1.35 - 1.0)/1.35 \approx 25\%$.

Returning to the influence of density-dependent growth, in the worst case, production would be overestimated, through neglect of this effect, by $100\% \times (1.0 - 0.65)/0.65 \approx 50\%$. (According to Rijnsdorp 1994, density-dependent growth seems to be more prominent in freshwater systems than in marine systems.) If one has evidence of strong density-dependent growth for a particular stock, production can be corrected by applying the reasoning above. In the absence of such information, one could apply the simple expedient of an a priori bias correcting reduction of $50\%/2 = 25\%$ which would ensure that the estimated \bar{P} suffered no worse than a 25% error caused by density-dependent growth.