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Bioenergetics, overcompensation, and the source–sink status of marine reserves

David Claessen, Anneke S. de Vos, and André M. de Roos

Abstract: One of the hypothesized functions of marine protected areas (MPAs) is to serve as sources of biomass, with biomass spilling over from the reserve into neighbouring, harvested areas. We argue that the net larval flow (from or to the marine reserve) depends on between-area differences in the population-level biomass production rate, whereas the direction of adult flow depends on differences in the biomass standing stock. Hence, an important question is whether population-level biomass production increases (overcompensation) or decreases (undercompensation) with increased per capita mortality. We show that in a consumer–resource context, the source–sink status of an MPA may depend on the details of the individual-level bioenergetics, as well as on the dispersal rates of larvae and adults. We compare two classic bioenergetic models (net-production vs. gross-production allocation). The net-production model predicts that population-level reproduction may increase with mortality (overcompensation), whereas gross-production allocation always results in undercompensation. We show that models often implicitly assume gross-production allocation, thus potentially overestimating the capacity of MPAs to source unprotected areas. We briefly discuss results of two other models (a simplified, logistic model and a size-structured model), suggesting that the relation between overcompensation and the larval sink status of MPAs is general.

Résumé : Une des fonctions présumées des zones de protection marine (« MPA ») est de servir de source de biomasse, cette biomasse débordant alors de la réserve vers les zones exploitées adjacentes. Nous soutenons que le flux net de larves (depuis ou vers la réserve marine) dépend des différences entre les deux zones du taux de production de la biomasse au niveau de la population, alors que la direction du flux des adultes dépend des différences de biomasse des stocks. Cela soulève une question importante à savoir si la production de biomasse au niveau de la population augmente (surcompensation) ou diminue (sous-compensation) en fonction d'une augmentation de la mortalité par individu. Nous démontrons que, dans un contexte de consommateurs et de ressources, le statut de source ou de piège d'une MPA peut dépendre des détails de la bioénergétique au niveau individuel, mais aussi des taux de dispersion des larves et des adultes. Nous comparons deux modèles bioénergétiques classiques (allocation de la production nette ou de la production brute). Le modèle de production nette prédit que la reproduction au niveau de la population peut augmenter en fonction de la mortalité (surcompensation), alors que l'allocation de la production brute entraîne toujours une sous-compensation. Nous montrons que les modèles présupposent souvent une allocation de la production brute, surestimant ainsi la capacité des MPA d'alimenter les zones non protégées. Nous discutons brièvement des résultats de deux autres modèles (un modèle logistique simple et un modèle structuré en fonction de la taille) et nous croyons que la relation entre la surcompensation et le statut des MPA comme pièges pour les larves est une relation générale.

[Traduit par la Rédaction]

Introduction

Marine reserves (or marine protected areas, MPAs hereafter) introduce a spatial heterogeneity into ecosystems that is caused by spatial variation in mortality rates of harvested populations. This results in an imbalance between protected and unprotected areas not only in terms of standing biomass of populations in the food web (Halpern and Warner 2002; Micheli et al. 2004b) but also, by consequence, in terms of ecological interactions, such as competition for resources, predation, etc. This imbalance is the driving force behind the potential of marine reserves to serve as biomass sources (through spillover) for the harvested areas, possibly leading to equal or even enhanced yield compared with conventional, effort-based fisheries management (Mangel 1998; Neubert 2003; Hart 2006). This simple vision of marine reserves suggests that two aspects are important for the dynamics of MPAs and surrounding areas: (i) the local ecological response of the food web to the presence or absence of harvesting, and (ii) the exchange of individuals through migration (Walters 2000; Mangel and Levin 2005). Mathematical models have been used to investigate the consequences of different assumptions on these two aspects for

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both the economic and conservational implications of MPAs (reviewed in Gerber et al. 2003; Baskett et al. 2007; Pelletier et al. 2008), including the roles of predation, competition, and mutualism (Baskett et al. 2007), spatial processes (Botsford et al. 2001; Guichard et al. 2004), juvenile–adult stage structure (St. Mary et al. 2000), and density-dependent growth (Gårdmark et al. 2006).

In this paper, we show that a fundamental but usually implicit assumption concerning individual-level energy allocation affects both aspects (*i*) and (*ii*) in a potentially important way, which has been ignored in most previous modelling work. We study two alternative, well-known models for individual-level bioenergetics. A bioenergetics model answers the question as to how much energy is allocated to growth, reproduction, and maintenance, given a quantity of food in the environment. In the literature, different models of energy allocation exist, which can be divided into two classes: gross-production allocation and net-production allocation. The distinction between the two classes is that reproduction is supposed to be proportional to the energy intake rate either before or after maintenance costs have been substracted. By consequence, the allocation models assume different behaviour at low food conditions: in the gross-production model, individuals reproduce as long as the food concentration is positive, whereas in the net-production model, there is a threshold food concentration below which individuals stop reproducing (Gurney et al. 1996). Simple MPA models formulated in terms of ordinary or partial differential equations (ODEs or PDEs, respectively) are often based on Lotka–Volterra type models (Neubert 2003; Steele and Beet 2003; Baskett et al. 2006), without explicitly considering bioenergetics. We show that such models are equivalent to an implicit assumption of gross-production allocation.

In the context of size-structured population models, Gurney et al. (1996) have shown that the individual-level energetics influence by which demographic process populations are regulated (i.e., reproduction, maturation, or survival limitation). The relevance of such individual-level assumptions in the context of MPAs is their implications for the local ecological response to the presence or absence of harvesting (aspect (*i*) above); the food web response will depend on how individuals react to (changes in) their environment. To illustrate this point, in this paper we study the consequences of different bioenergetic assumptions embedded in a simple food web consisting of a harvested consumer population (without size structure) and its resource population, based on the model of Yodzis and Innes (1992). Space is divided into a protected area and a harvested area, between which consumers (but not the resource) are assumed to migrate. Our model allows the dispersal rates of larvae and adults to be tuned independently. Density dependence results from competition for, and depletion of, the resource. The resource density inside and outside the MPA influences the energy budget and hence the respective rates of biomass growth and reproduction of the consumers in the two areas.

We thus address the question of how density-dependent food limitation, and its consequences for growth and reproduction, will affect projected effects of spillover from marine reserves. One of the hypothesized functions of marine protected areas (MPAs) is to serve as sources of biomass, with biomass spilling over from the MPA into neighbouring,

harvested areas. We show that in a consumer–resource context, the source–sink status of the MPA may depend on the details of the individual-level bioenergetics, as well as on the dispersal rates of larvae and adults. We investigate the robustness of our model results by comparing the results with two alternative models: a simpler one (based on the logistic model) and a more complex one (a size-structured model). The latter is of relevance as the origin of the energy allocation models lies in the context of size-structured models. In particular, size-structured models allow for different kinds of population regulation (maturation vs. reproduction limitation; de Roos et al. 2007), which may have consequences for the success of marine reserves.

The model

We model the biomass dynamics of a harvested fish population and its forage base, taking into account the consumer–resource interaction between these two populations, as well as a simple representation of the bioenergetics underlying the fish biomass dynamics. To introduce the notation, we first present a spatially undivided version of the model, based on Yodzis and Innes (1992). The biomass dynamics of the fished stock (*C* for consumer) and its forage base (*R* for resource) are modelled as follows:

$$(1) \qquad \frac{\mathrm{d}C}{\mathrm{d}t} = g(R)C + b(R)C - \delta C$$

$$(2) \qquad \frac{\mathrm{d}R}{\mathrm{d}t} = \rho(R_{\max} - R) - j(R)C$$

where *C* and *R* are biomass per unit of sea surface area. The fish dynamics are governed by biomass production though somatic growth $g(R)$ and birth $b(R)$, which depend on the current food density *R*, and mass-specific fish mortality, which is denoted by δ. The forage base *R* follows semi-chemostat dynamics with dilution rate ρ and maximum resource density $R_{\max}$. The function $j(R)$ is the mass-specific functional response of fish.

Note that $g(R)$ and $b(R)$ are production rates per unit of standing stock biomass. Below we make frequent use of the population-level production rates, which are defined as $G = g(R)C$ and $B = b(R)C$, respectively.

Energy budget: biomass growth, reproduction, and maintenance

The birth and somatic growth terms ($b(R)$ and $g(R)$) are based on simple bioenergetic considerations, based on the model of Yodzis and Innes (1992). Their model assumes that the production rate of biomass depends on the mass-specific ingestion rate ($j(R)$), the loss rate due to maintenance costs (m), and the loss rate due to mortality (δ):

$$(3) \qquad \frac{\mathrm{d}C}{\mathrm{d}t} = C[\sigma j(R) - m - \delta]$$

where $1 - \sigma$ is the fraction lost as feces and urine between ingestion and the metabolizable energy level. We assume that the consumer intake rate, $j(R)$, follows either a type-I or a type-II functional response, i.e., respectively,

$$(4) \quad j(R) = aR \quad \text{or} \quad j(R) = \frac{R}{R_h + R} j_{max}$$

where a is an attack rate, R_h is the half-saturation density, and j_{max} is the maximum intake rate. The Yodzis and Innes model (eq. 3) may be a sufficient description of the bioenergetics for a single population (in spite of its simplicity in terms of the absence of size or stage structure (de Roos et al. 2007) or energy storage (Kooijman 2000)). Yet for spatially subdivided populations with larval dispersal, such as in the case of marine reserves, it is necessary to at least specify the allocation of resources between reproduction, maintenance, and growth, because we need to know which part of the biomass production will be redistributed in the form of larval dispersal over the spatial range of the population.

Net-production allocation vs. gross-production allocation

Maintenance, reproduction, and somatic growth all derive from the assimilation rate, $\sigma j(R)$ (Kooijman 2000). Two major types of energy allocation models have been proposed, which are referred to as net-production allocation and gross-production allocation (Gurney et al. 1996; Nisbet et al. 2004). The rate of net production per unit of biomass equals the difference between the energy intake rate and the loss rate due to maintenance, $\sigma j(R) - m$, whereas gross production equals $\sigma j(R)$. Under net-production allocation, it is assumed that a fraction κ of the net production rate is allocated to somatic growth, and the fraction $1 - \kappa$ is used for reproduction. For the net-production allocation model, the rates of biomass production through somatic growth (g) and reproduction (b) then equal

$$(5) \quad \begin{aligned} g(R) &= (\sigma j(R) - m)\, \kappa \\ b(R) &= (\sigma j(R) - m)\,(1 - \kappa) \end{aligned}$$

For this model, it is necessary to specify what happens in case of starvation. In the MPA model specified below, it is possible that biomass flow increases local competition to such an extent that net production becomes negative in one of the areas. In this case, we assume that the birth rate b becomes zero, and the somatic growth rate g becomes equal to the (negative) net production rate. This amounts to assuming that in case of starvation, standing biomass is converted to cover maintenance.

Under gross-production allocation, it is assumed that a fraction κ of the gross production rate is used for both maintenance and somatic growth, and the fraction $1 - \kappa$ is allocated to reproduction, which is also referred to as the "kappa rule" model (Kooijman 2000). So for the gross-production allocation model, the rates of biomass production through somatic growth (g) and reproduction (b) are

$$(6) \quad \begin{aligned} g(R) &= \sigma j(R)\kappa - m \\ b(R) &= \sigma j(R)\,(1 - \kappa) \end{aligned}$$

Note that a special rule for starvation is unnecessary in the gross-allocation model: in case of starvation, the birth rate is still positive, and standing biomass is used to cover maintenance. Although a special rule for starvation may be more realistic for any particular fish species, we choose to use this simple assumption.

An important difference between the net- and gross-production models is hence their behaviour at low food

density: in the former model (eq. 5), reproduction and somatic growth stop simultaneously at a critical low food density, whereas in the latter model (eq. 5), growth stops but reproduction continues.

Note that for a spatially undivided population, the two models result in exactly the same total biomass dynamics, as all that matters is the sum of $b(R)$ and $g(R)$ (eq. 1). For both allocation models, we then obtain eq. 3.

We point out that in the gross-production allocation model, maintenance is equivalent to a local rate of biomass loss, similar to a mortality rate. At the population level, maintenance can hence be incorporated into a general loss term $\delta' = m + \delta$. MPA models that do not explicitly consider bioenergetics simply redistribute the population-level reproduction rate $B = b(R)C$ over protected and harvested areas, without discounting the maintenance costs. This amounts to the implicit assumption that maintenance costs are either absent or incorporated in the mortality loss term. In other words, ignoring bioenergetics corresponds to assuming implicitly gross-production allocation. Note also that assuming the absence of maintenance costs ($m = 0$) is equivalent to the gross-production model.

Spatial structure: marine reserve and fished area

Next we subdivide the consumer–resource system into a marine reserve and a harvested area. Adults (i.e., standing biomass) suffer a per-unit biomass harvesting mortality in the fished area, denoted by H. The protected area is assumed to cover a fraction x of the total area A. The fraction α of produced consumer larvae is assumed to migrate and to be equally redistributed between the areas. Adults migrate with rate β. Note that larval migration amounts to a redistribution of the birth rate, whereas adult migration amounts to a redistribution of standing stock biomass. The so-called larval pool equal redistribution (LPER) assumption is equivalent to setting $\alpha = 1$ and $\beta = 0$.

Variables and population-level rates pertaining to the protected and the harvested areas are denoted by indices 1 and 2, respectively. For example, the population-level birth rates are now defined as $B_1 = b(R_1)C_1$ and $B_2 = b(R_2)C_2$, respectively. Because all variables are expressed as densities per unit of sea surface area, the total biomass in the protected and fished areas equals C_1Ax and $C_2A(1 - x)$, respectively.

Biomass flow between areas: source and sink

The dynamics in the two areas depend on the biomass flow of larval and adult biomass. Assuming that from both areas, a fraction α of produced larvae enters a common dispersal pool, the rate of larval settlement in each area equals the sum of local larvae production, $(1 - \alpha)B_i$, and the inflow of larvae from the dispersal pool, $\alpha[xB_1 + (1 - x)B_2]$. This corresponds to the widely used LPER assumption. The larval settlement rate in the protected area is then, after simplification,

$$(7) \quad S_1 = B_1 - \alpha(1 - x)(B_1 - B_2)$$

For the fished area, the equivalent rate is

$$(8) \quad S_2 = B_2 + \alpha x(B_1 - B_2)$$

These equations show that the larval settlement rate exceeds the local birth rate in the area with the lowest local birth

rate. In other words, the net larval flow is always from the most productive to the least productive area. The net larval flow from the reserve to the harvested area (denoted by f_L) equals the difference between inflow and ouflow in the harvested area, multiplied by the size of the harvested area:

$$(9) \qquad f_L = \{\alpha[xB_1 + (1-x)B_2] - \alpha B_2\}(1-x)A$$
$$= \alpha x(1-x)A(B_1 - B_2)$$

The flow is positive, i.e., from the reserve to the harvested area, if and only if the reserve is more productive (per unit of sea area) than the fished area ($B_1 > B_2$).

Similar to larval migration, adults are assumed to migrate with rate β and to enter a common dispersal pool, which is then equally redistributed. Although this way to model adult migration is less standard than for larvae, the resulting equation is completely analogous to the more commonly used diffusive model.

We obtain expressions similar to larval migration. For example, in the reserve, the rate of departing biomass equals βC_1 and the rate of incoming biomass equals $\beta[xC_1 + (1 - x)C_2]$. The migration balance thus equals $-\beta(1 - x)(C_1 - C_2)$ in the reserve and $\beta x(C_1 - C_2)$ in the harvested area. The net biomass flow due to adult migration is again found by multiplication of either of these by the corresponding surface area:

$$(10) \qquad f_A = \beta x(1-x)A(C_1 - C_2)$$

The flow is positive, i.e., spillover from the reserve to the harvested area, if and only if the biomass density is highest in the reserve ($C_1 > C_2$).

Note that the direction of the larval flow depends on differences in the biomass production rate, whereas the direction of adult flow depends on differences in the biomass standing stock. The two flows do not necessarily point in the same direction. The net total biomass flow equals their sum $f_{tot} = f_L + f_A$.

The full MPA model

Extending eqs. 1–2 to two areas and substituting the migration terms, we obtain

$$(11) \qquad \frac{dC_1}{dt} = G_1 + B_1 - \alpha(1-x)(B_1 - B_2)$$
$$-\beta(1-x)(C_1 - C_2) - C_1\delta$$

$$(12) \qquad \frac{dC_2}{dt} = G_2 + B_2 + \alpha x(B_1 - B_2) + \beta x(C_1 - C_2)$$
$$-C_2(\delta + H)$$

$$(13) \qquad \frac{dR_1}{dt} = \rho(R_{max} - R_1) - j(R_1)C_1$$

$$(14) \qquad \frac{dR_2}{dt} = \rho(R_{max} - R_2) - j(R_2)C_2$$

The dynamics of the fish populations (C_1 and C_2) are the sum of four terms: local growth of standing biomass, larval production and redistribution, adult migration, and mortality. Note that we assume that the food base (R_1 and R_2) does not migrate.

Parameter values

The default parameter values of the consumer–resource model are based on the equivalent but stage-structured model of de Roos et al. (2007): $j_{max} = 6$, $m = 1$, $\sigma = 0.7$, $\rho = 0.5$, $R_h = 1$. The natural mortality rate is assumed to be $\delta = 0.1$, which represents a typical value on a per-year basis for marine fish populations (Andersen and Ursin 1977). We have, however, tested the model behaviour over a range of δ up to 1. We obtain qualitatively similar results in all cases, although increasing δ decreases standing stock biomass and adult flow and makes the larval flow less negative. In our simulations presented below, we vary the harvesting rate H. We note, however, that rough estimates of harvesting mortality fall in the range of 2–10 times the natural mortality rate (Pope et al. 2006). With a mortality rate of $\delta = 0.1$, appropriate harvesting rates (H) thus fall in the range of 0.2 to 1. The larval migration parameter α is varied between 0 and 1 (note that α is a proporion). The adult migration parameter β should be interpreted relative to the mortality parameter: on average, an unharvested individual is expected to migrate β/δ times during its life time. We vary β between 0 and 1.

Results

Consequences of choice of allocation model

To understand how the MPA system reacts to harvesting mortality, it is instructive to first analyse the how the equilibrium of the single-area system (eqs. 1–2) without dispersal depends on the level of mortality, δ. Recall that for a single population, the allocation into growth and reproduction is irrelevant, as it is their sum that appears in eq. 1.

To simplify the analysis, we initially assume a linear functional response, which does not qualitatively influence the results (see below). For the single-area system (eqs. 1–2), the equilibrium equals

$$(15) \qquad \tilde{C} = \frac{\rho(\sigma a R_{max} - m - \delta)}{a(m + \delta)}$$

$$(16) \qquad \tilde{R} = \frac{m + \delta}{\sigma a}$$

These equations show that $\tilde{C}$ decreases and $\tilde{R}$ increases with mortality, because $\partial\tilde{C}/\partial\delta < 0$ and $\partial\tilde{R}/\partial\delta > 0$. The fish population goes extinct when mortality exceeds the value

$$(17) \qquad \delta_{ext} = \sigma a R_{max} - m$$

The equilibrium (eqs. 15–16) is the same for the two allocation rules (eqs. 5–6). However, this is not true for the steady-state total reproduction rate, denoted by $\tilde{B}$. With net-production allocation,

$$(18) \qquad \tilde{B} = \delta(1 - \kappa)\tilde{C}$$

with $\tilde{C}$ as defined in eq. 15, whereas with gross-production allocation,

$$(19) \qquad \tilde{B} = (m + \delta)(1 - \kappa)\tilde{C}$$

An important difference between the allocation rules is the resulting relation between the total reproduction rate and (mass-specific) mortality. By substituting eq. 15 into eq. 19,

we find that with gross-production allocation, the reproduction rate necessarily decreases with mortality, i.e., $\partial \tilde{B}/\partial \delta < 0$. Yet with net-production allocation, the curve of $\tilde{B}$ over mortality is dome-shaped; it first increases between $\delta = 0$ and a critical mortality rate δ_{crit}, after which it decreases to zero at δ_{ext}. The critical mortality rate is as follows:

$$(20) \qquad \delta_{\mathrm{crit}} = -m + \sqrt{\sigma a R_{\max}\, m}$$

This equation shows that with $m > 0$, the population-level birth rate can increase with mortality, even though the equilibrium biomass $\tilde{C}$ always decreases with mortality. We refer to such a postive relation between total reproduction and mortality as "overcompensation".

The explanation of the overcompensation lies in (*i*) the resource dependence of the reproduction rate and (*ii*) the balancing of the birth and mortality rates in equilibrium. Increasing mortality decreases competition for the resource, which increases the reproduction rate per unit of biomass. Yet the total (population) reproduction rate may still decrease if the standing biomass decreases faster than the fecundity increases. This is the case when reproduction is proportional to the intake rate and hence to the resource density, as in the gross-production model. However, when reproduction is proportional to the net-production rate, by contrast, fecundity can increase much faster than the resource density itself. This becomes obvious in the limit of zero mortality. The equilibrium condition $\mathrm{d}C/\mathrm{d}t = 0$ requires that net production balances the death rate, i.e., $\sigma j(\tilde{R}) - m = \delta$, which means that for $\delta = 0$, the net-production rate is zero. This, in turn, means that the total reproduction rate $\tilde{B}$ is zero for $\delta = 0$. $\tilde{B}$ then necessarily increases with δ.

In summary, overcompensation is never found in the gross-production model, whereas it occurs in the net-production model whenever the background mortality is relatively low ($\delta < \delta_{\mathrm{crit}}$). This result is true also for a type-II functional response, but the equation of δ_{crit} is very ugly in that case. A graph of δ_{crit} for a type-II functional response, plotted against m (Fig. 1), shows that overcompensation is likely to occur with plausible parameter values; across a range of taxa, the mortality rate appears to be of the order of 10% of the maintenance rate (de Roos et al. 2007). Figure 1 illustrates that for this estimation, most combinations of δ and m fall in the region of overcompensation. Very similar results are obtained when varying the parameters $R_{\max}$, a, and R_{h} (data not shown).

Implications for the MPA model

The analysis of the single-area model gives an idea of how the MPA model will behave. As a simple thought experiment, compare the two areas of the MPA model, without any migration and with a low harvesting rate. The analysis tells us that the standing biomass will be lower in the harvested area, for either allocation model. Assuming gross-production allocation, we also know that the total birth rate will be lower in the harvested area. So we expect that allowing either larval migration between the two areas or adult migration will result in a biomass flow from the reserve into the harvested area (i.e., $f_{\mathrm{L}} > 0$ and $f_{\mathrm{A}} > 0$).

Next, consider the net-allocation model. Because of the overcompensation, the total birth rate is then likely to be

Fig. 1. The regions of overcompensation, undercompensation, and extinction in m,δ-parameter space for the spatially undivided model (eqs. 1–2) assuming net-production model and a type-II functional response. Without maintenance ($m = 0$), being the analogous case of gross production, we obtain undercompensation for all values of the mortality rate except zero. For comparison with the MPA model (eqs. 11–14), we have indicated for the MPA model with $\alpha = 1$ and $\beta = 0$, the curves where larval flow $f_{\mathrm{L}} = 0$, assuming $F = 1$ (broken line) or $F = 0.1$ (dotted line), respectively. Parameters: $\kappa = 0.5$, $j_{\max} = 6$, $R_{\mathrm{h}} = 1$, $\sigma = 0.7$, $\rho = 0.5$, $R_{\max} = 5$, $x = 0.3$.
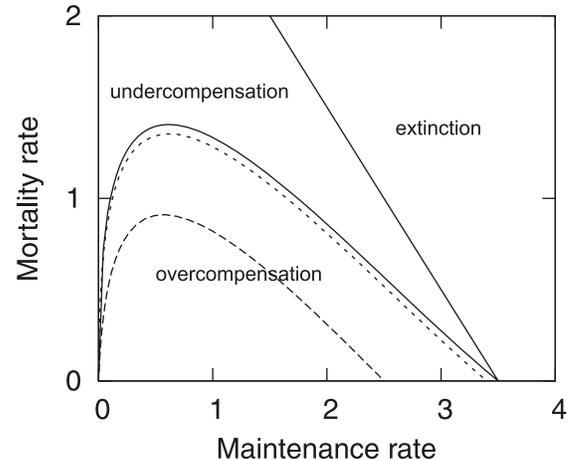
higher in the harvested area than in the MPA. Larval migration is hence likely to result in a biomass flow from the harvested area into the reserve ($f_{\mathrm{L}} < 0$). With net-production allocation, we therefore expect the MPA to be a biomass sink for larvae.

However, these expectations should be checked with analysis of the full MPA model, as the steady state of the full model with migration does not necessarily conform to our intuition based on the limiting case of no migration.

The MPA model: source–sink status of the reserve

Here we study the dynamics of the full MPA system (eqs. 11–14) assuming a type-II functional response. We compute the steady state of the MPA model over a range of the harvesting rate H (similar to Fig. 2), with the MPA being 30% of the total area ($x = 0.3$).

Model analysis confirms the intuition on the gross-production allocation model (Fig. 3). Assuming larval migration only ($\alpha = 1$, $\beta = 0$), the standing biomass decreases with H in both the protected and harvested areas, but is consistently higher in the protected area ($C_1 > C_2$). The same is true for the population birth rates (i.e., undercompensation and $B_1 > B_2$), despite increasing resource density in both areas. The resulting biomass flow is positive; the MPA is a source of larval production. Note also that the MPA prevents the harvested population from going extinct at high harvesting rates (cf. Fig. 2).

Model analysis also confirms the intuition on the net-allocation model (Fig. 4). The populaton birth rate in the harvested area displays the typical pattern of overcompensation (cf. Fig. 2). By contrast, the birth rate in the protected area decreases and is zero over a considerable range of H. In this range, the consumers in the MPA are

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Fig. 2. Steady state of the spatially undivided version of the model (eqs. 1–2). Top panel: consumer ($\tilde{C}$; solid line) and resource ($\tilde{R}$; broken line) biomass density. Middle panel: population birth rate $\tilde{B}$ for the net-production (solid line) and gross-production (broken line) models. Bottom panel: yield. All quantities are per unit of surface area. Parameters: $\kappa = 0.5$, $j_{max} = 6$, $R_h = 1$, $m = 1$, $\sigma = 0.7$, $\delta = 0.1$, $\rho = 0.5$, $R_{max} = 5$.
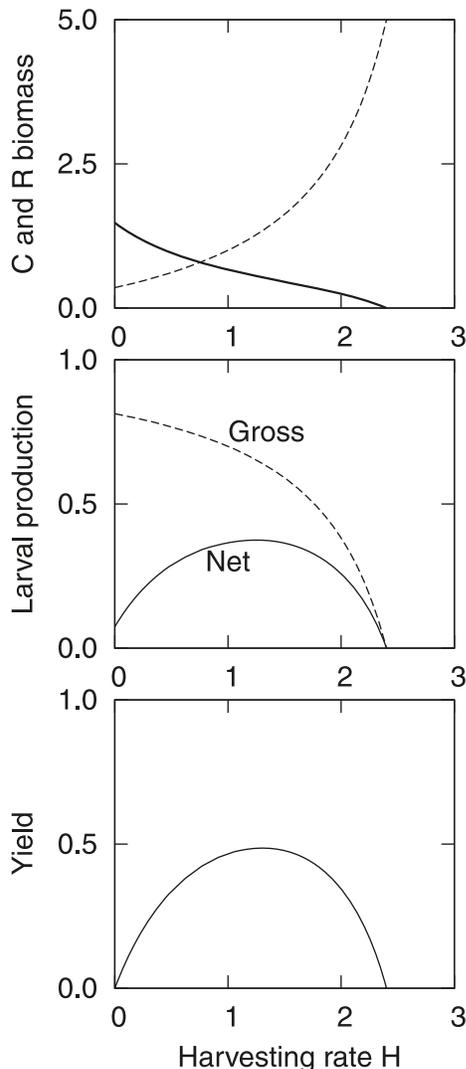
starving due to severe resource competition. Throughout the range where $B_1 < B_2$, the larval flow is negative (Fig. 4). The reserve is thus a larval sink for harvesting rates up to the point at which the harvested population would go extinct in the absence of an MPA (cf. Fig. 2). Beyond this point, the fished stock is practically extinct, and the MPA becomes a source of larvae, saving the harvested population from true extinction.

In the marine reserve, the biomass initially increases with H, mirrorring the pattern of larval production in the harvested area (Fig. 4). Although the resource in the exploited area increases gradually with H, converging to its carrying capacity at very high H, in the reserve, the resource first decreases with H, showing that competition for food intensifies in the MPA. In fact, the strong inflow of larvae causes an unsustainably high biomass density in the MPA: severe re-

source competition leads to starvation, most notably resulting in the complete absence of reproduction inside the MPA.

The idea is thus that overcompensation in the harvested area causes the MPA to be a larval sink. We test this idea by drawing the curve for which the larval flow is zero (Fig. 1), which delimits the region in which the MPA is a sink (i.e., below the broken or dotted curves). The figure shows that with decreasing H, the sink region approximates the region of overcompensation, thus confirming the idea. Note that with increasing H, the sink region becomes smaller, which reflects the fact that the sink status of the MPA depends on H and is obtained for small and intermediate H only (Fig. 4).

The effect of adult migration

Allowing adults to migrate ($\beta > 0$) results in an additional biomass flow, which is always directed from the MPA to the harvested area, because $C_1 > C_2$ (cf. eq. 10). Here we study the effect of adult migration on the larval flow (f_L) and total flow (f_{tot}).

Consider the example with $\alpha = 1$ and $\beta = 0.5$ (Fig. 5). (Note that $\beta/\delta = 5$, meaning that unharvested adults migrate on average five times in a life time.) The flow of standing biomass changes the pattern of consumer biomass in the reserve; C_1 now decreases monotonically with H. The adult flow releases the resource competition in the MPA, allowing for reproduction in that area. Initially, however, reproduction is still higher in the harvested area ($B_1 < B_2$), resulting in negative larval flow up to $H \approx 3$. In this range, the MPA is hence a sink for larvae, but a source of adults. Overall, the MPA is a source of biomass ($f_{tot} > 0$).

Next we study the effect of adult migration on the source–sink status of the MPA systematically (Fig. 6a). Figure 6 depicts the regions in H, β-parameter space where the MPA is a sink of total biomass and (or) larvae. These zones are delimited by the curves of $f_L = 0$ and $f_{tot} = 0$. The curve of $f_L = 0$ is almost vertical, indicating that the rate of adult migration has little influence on the sign of the larval flow. The MPA is a larval sink even for very high values of β. By contrast, the total biomass flow depends strongly on β: increasing adult migration reduces the range of H with negative total flow. The region marked "S" shows that starvation in the MPA, and hence zero reproduction, is restricted to low adult migration.

The effect of larval migration

The effect of changing the proportion of dispersing larvae (α) mirrors the effect of changing adult migration. For fixed adult migration ($\beta = 0.1$), reducing α has no influence on the sign of the larval flow (Fig. 6b). As expected, the total biomass flow becomes positive when larval migration becomes very small. Starvation is limited to very high larval migration.

The effect of the size of the MPA

The relative size of the reserve (x) determines the relative contribution of the two areas to the biomass flows; increasing x hence decreases the potential effect of overcompensation, which occurs in the harvested area only, on the larval flow. Changing x may influence the direction of the larval flow (f_L); if the MPA is larger, the larval flow is negative

Fig. 3. The equilibrium of the MPA model (eqs. 11–14) with gross-production allocation and larval migration only ($\alpha = 1$, $\beta = 0$). In a, b, and c, broken lines represent the marine reserve; solid lines, the harvested area. (a) Consumer population biomass and yield (dotted line); (b) resource biomass; (c) larval production $\tilde{B}_1$ and $\tilde{B}_2$; (d) net biomass flow (thick solid line; equal to larval flow) from MPA to harvested zone and adult flow (dotted line; equal to zero). Parameters: $x = 0.3$, $\kappa = 0.5$, $j_{max} = 6$, $R_h = 1$, $m = 1$, $\sigma = 0.7$, $\delta = 0.1$, $\rho = 0.5$, $R_{max} = 5$.
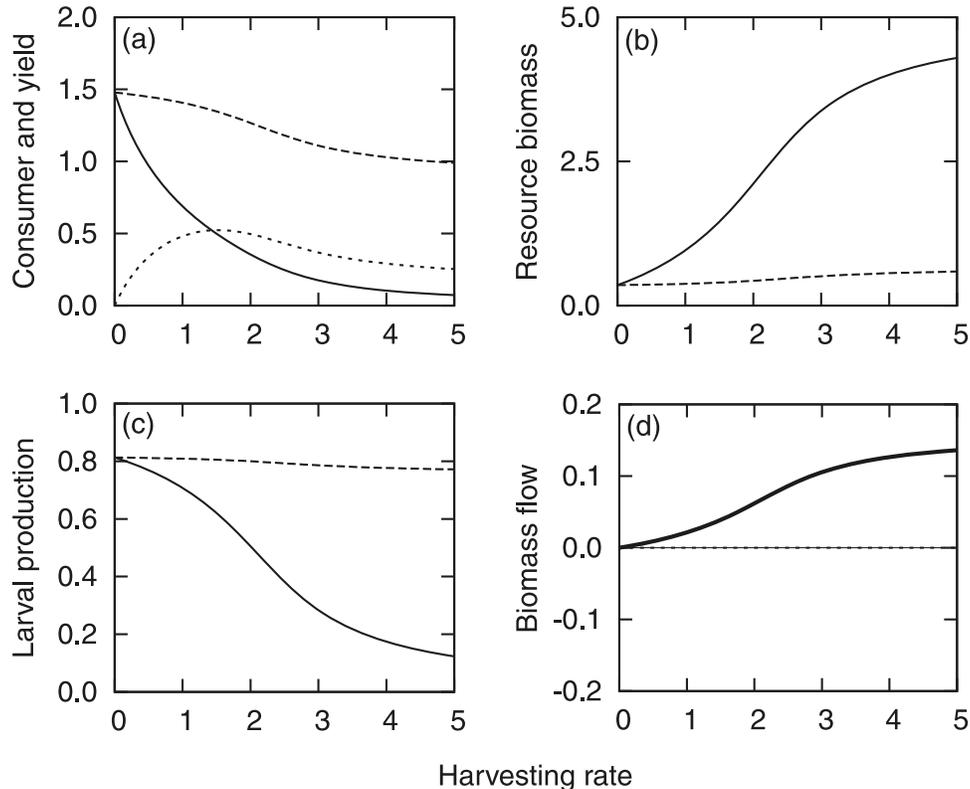
over a wider range of H (Fig. 7). At high H, small reserve size accentuates the "source" potential of marine reserves, as most of the locally produced larvae are lost to migration, thus reducing resource competition in the reserve and increasing the birth rate $\tilde{B}_1$. However, at low and intermediate H, when overcompensation is strong in the harvested area (Fig. 4), small reserve size accentuates the "sink" potential of an MPA. With small x, the larval flow is largely determined by the harvested area such that overcompensation has a large impact on the dynamics in the MPA. By consequence, the starvation range is limited to small MPA size (Fig. 7).

Changing x does not, however, influence the sign of the total biomass flow (Fig. 7). This "inertia" is independent of the values of the other parameters (data not shown). The inertia can be understood as follows: when the total biomass flow is zero, each unit of sea area has a zero net flow. Given that the biomass inflow (larvae + adults) is the same for each unit of sea surface area, the biomass outflow per unit area (larvae + adults) must be the same in the MPA and the harvested area. Changing the relative contribution (x) to the common dispersal pool then has no effect whatsoever.

Alternative models
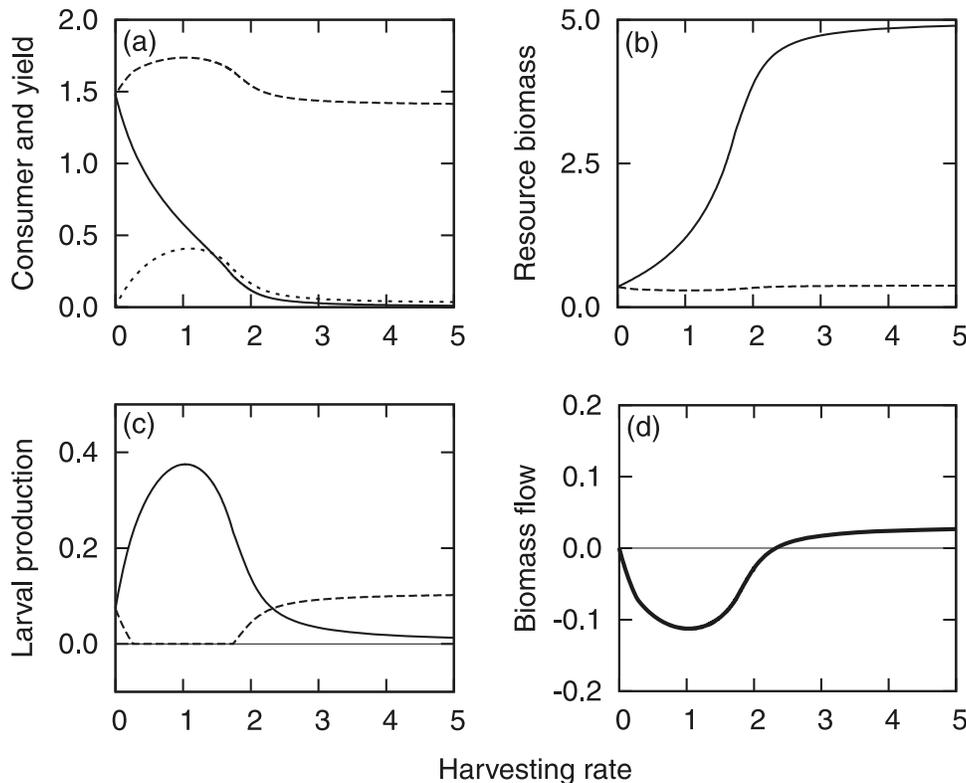
Size-structured population model

The allocation models studied in this paper were originally designed for size-structured population models (Gurney et al. 1996). In size-structured population models,

density dependence may affect not only fecundity, settlement, and survival, but also maturation and individual growth. To illustrate the consequences of size structure, we analyse a well-studied size-structured population model in the context of our findings above.

The gross-production allocation model (eq. 6) first appeared as the kappa rule in a size-structured population model (Kooijman and Metz 1984). The Kooijman–Metz model has since been studied in various forms, and here we use the model published by de Roos and Persson (2002), but without predators. We extend their model by including an MPA and larval dispersal (analogous to eqs. (11–14) with $\alpha = 1$ and $\beta = 0$). In this model, individuals are born with size ℓ_b and mature at size ℓ_j. The gross-production model results in von Bertalanffy growth with asymptotic size $\ell_m R/(R_h + R)$. A model description (without MPA) can be found in de Roos and Persson (2002).

We do not present a full analysis of the size-structured model, but merely illustrate the implications of a juvenile life stage. In the size-structured model (without MPA), the consumer and resource biomass (Fig. 8a) follow the same pattern as in the unstructured model (cf. Fig. 2). Surprisingly, however, we find overcompensation (Fig. 8b), despite the gross-production allocation model. Based on the overcompensation, we thus expect a negative biomass flow (from the harvested area to the MPA) in the case of larval migration. Including an MPA in the size-structured model (with $x = 0.3$) confirms this expectation (Fig. 8c).

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Fig. 4. The equilibrium of the MPA model (eqs. 11–14) with net-production allocation and larval migration only ($\alpha = 1$, $\beta = 0$). In a, b, and c, broken lines represent the marine reserve; solid lines, the harvested area. (a) Consumer population biomass and yield (dotted line); (b) resource biomass; (c) larval production $\tilde{B}_1$ and $\tilde{B}_2$; (d) larval flow f_L from MPA to harvested area (negative flow means reserve is larval sink). Parameters: $x = 0.3$, $\kappa = 0.5$, $j_{max} = 6$, $R_h = 1$, $m = 1$, $\sigma = 0.7$, $\delta = 0.1$, $\rho = 0.5$, $R_{max} = 5$.

Which difference between the unstructured and structured models explains the found overcompensation? An important difference between unstructured and size-structured models is that the latter allows for different kinds of population regulation, depending on which demographic process (juvenile growth–maturation or adult reproduction) is most affected by intraspecific competition and hence limiting population growth. If a population is maturation-limited (as in Figs. 8a–8b), then increasing the mortality rate releases the competition among juveniles, and the adult biomass increases due to increased maturation (de Roos et al. 2007). In this case, we thus observe an overcompensation of the adult standing biomass: adult biomass increases with mortality (Fig. 8a, thin solid line), resulting in an overcompensation of the population-level reproduction rate (Fig. 8b). To demonstrate the crucial role of the juvenile life stage, we have rerun the model with $\ell_j < \ell_b$, such that individuals are born mature (Figs. 8d–8f). In this case, the population is necessarily reproduction-limited. Without a juvenile stage, the size-structured model predicts undercompensation (Fig. 8e). The corresponding MPA model displays a positive biomass flow (Fig. 8e), as expected from the undercompensation.

This simple example illustrates that maturation limitation in structured populations may lead to overcompensation in both adult biomass and the population reproduction rate, as shown by de Roos et al. (2007). The examples demonstrate that (i) overcompensation is not restricted to net-production allocation models and (ii) overcompensation in a model

without MPA implies a negative larval biomass flow in the corresponding MPA model, whatever mechanism is causing the overcompensation. The size-structured model thus suggests that the association of overcompensation and negative biomass flow is general.

Logistic MPA model

Now that we have identified the role of overcompensation, we can check that it works in the simplest model that could produce such a result, the logistic growth model:

$$(21) \quad \frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)$$

To be able to use the death rate as an independent parameter and to use the total birth rate as a model output, we have to decompose eq. 21 by making assumptions about how it reflects underlying per capita birth and death rates. As in the previous two models, we assume that density dependence affects the birth rate, whereas the death rate remains constant. By choosing $b - \beta N$ for the per capita birth rate and d for the death rate, we obtain,

$$(22) \quad \frac{dN}{dt} = N(b - \beta N - d)$$

which is equivalent to eq. 21 with $r = b - d$ and $K = (b - d)/\beta$.

The equilibrium population of eq. 22 equals $\tilde{N} = (b - d)/\beta$. The population-level birth rate, defined as $\tilde{B} = \tilde{N}(b - \beta N)$, thus equals

Fig. 5. The equilibrium of the MPA model (eqs. 11–14) with net-production allocation and both larval and adult migration ($\alpha = 1$, $\beta = 0.5$). In a, b, and c, broken lines represent the marine reserve; solid lines, the harvested area. (a) Consumer population biomass and yield (dotted line); (b) resource biomass; (c) larval production $\tilde{B}_1$ and $\tilde{B}_2$; (d) larval flow (broken line), adult flow (dotted line), and net biomass flow (thick solid line) from MPA to harvested zone. Parameters: $x = 0.3$, $\kappa = 0.5$, $j_{max} = 6$, $R_h = 1$, $m = 1$, $\sigma = 0.7$, $\delta = 0.1$, $\rho = 0.5$, $R_{max} = 5$.
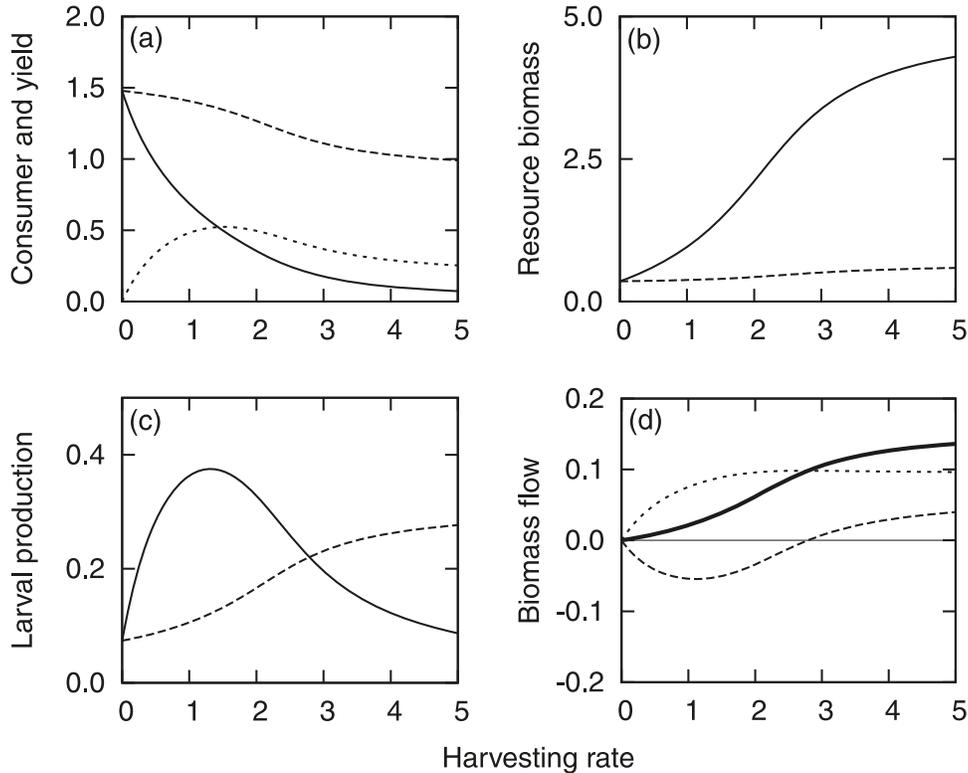
$$(23) \quad \tilde{B} = d\,\frac{b - d}{\beta}$$

Because $\tilde{B}$ goes to zero when d goes to zero, the logistic growth model clearly displays overcompensation for any value of b and β. Based on this observation, we expect that an MPA model that connects two logistic equations with larval dispersal will predict that the MPA is a larval sink. To check this prediction, we have extended eq. 22 by including a second harvested population and assuming LPER. We have computed its steady state and the corresponding direction of the larval biomass flow. The results are analogous to the ones obtained with the consumer–resource model above and confirm that the logistic model indeed predicts the MPA to be a larval sink for d below a critical background mortality rate (data not shown).

If, however, we assume that density dependence does not influence the birth rate but the death rate (by choosing $d + \beta N$ for the death rate and b for the birth rate), we obtain $\tilde{B} = b(b - d)/\beta$, which corresponds to undercompensation. Thus, overcompensation requires that density dependence affects the birth rate.

Discussion

Our main result is that the source–sink status of marine reserves depends on the effect of the per capita mortality rate, including harvesting mortality, on the population-level reproduction rate (B). If this relation displays overcompensation (i.e., B initially increases with mortality), then any de-
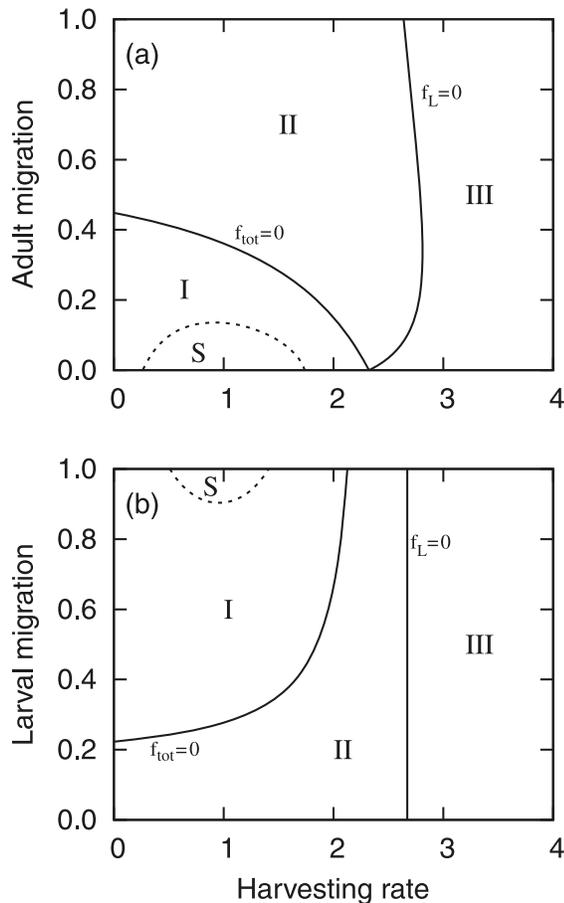
gree of larval migration results in a net biomass flow of larvae from the harvested area into the MPA, and the MPA is thus a sink of larval biomass. In the case of undercompensation, by contrast, the MPA is a source of larval biomass.

Why do MPAs become larval sinks? The explanation resides in intraspecific competition. Competition is more severe inside the MPA due to the reduced mortality rate (e.g., see the lower resource density R_1 in Fig. 3). When increased competition reduces the population-level reproductive output (i.e., overcompensation of B), then total reproduction is higher outside the MPA than inside. By consequence, the net larval flow will be towards the MPA. This, however, is not true for populations that display undercompensation of B (such as the gross-production model (eq. 6)).

For migration of standing biomass (as opposed to larval migration), our results suggest that marine reserves are usually a source of biomass, if it is assumed (as done here) that net migration goes from high-biomass to low-biomass areas. Larval and adult flow may thus be in opposite directions, and the net effect obviously depends on the relative rates of larval and adult migration. It should be noted, however, that in size-structured populations, adult biomass may itself display overcompensation, i.e., increase with mortality (de Roos et al. 2007). This may hence cause an MPA to be a sink of adult fish.

The main work presented here concerns the effect of alternative bioenergetic models on the source–sink status of MPAs. The conclusion is that gross-production allocation results in undercompensation of the population reproduction

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Fig. 6. The effect of migration on the source–sink status of the MPA model (eqs. 11–14) with net-production allocation. Top panel: the effect of adult migration (β) for fixed larval migration ($\alpha = 1$). Bottom panel: the effect of larval migration (α) with fixed adult migration ($\beta = 0.1$). Solid lines indicate zero larval flow ($f_L = 0$) and zero total biomass flow ($f_{tot} = 0$). The dotted line ($\tilde{B}_1 = 0$) delimits the region with starvation in the MPA (zone S). Zones: I, MPA is sink of larvae and of net biomass; II, MPA is sink of larvae but source of net biomass; III, MPA is source of larvae and of net biomass. Parameters: $x = 0.3$, $\kappa = 0.5$, $j_{max} = 6$, $R_h = 1$, $m = 1$, $\sigma = 0.7$, $\delta = 0.1$, $\rho = 0.5$, $R_{max} = 5$.

Fig. 7. The effect of relative reserve size (x) on the source–sink status of the MPA model (eqs. 11–14) with net-production allocation for $\beta = 0.1$ and $\alpha = 1$. Solid lines indicate zero larval flow ($f_L = 0$) and zero total biomass flow ($f_{tot} = 0$). The dotted line ($\tilde{B}_1 = 0$) delimits the region with starvation in the MPA (zone S). Zones: I, MPA is sink of larvae and of net biomass; II, MPA is sink of larvae but source of net biomass; III, MPA is source of larvae and of net biomass. Parameters: $\kappa = 0.5$, $j_{max} = 6$, $R_h = 1$, $m = 1$, $\sigma = 0.7$, $\delta = 0.1$, $\rho = 0.5$, $R_{max} = 5$.
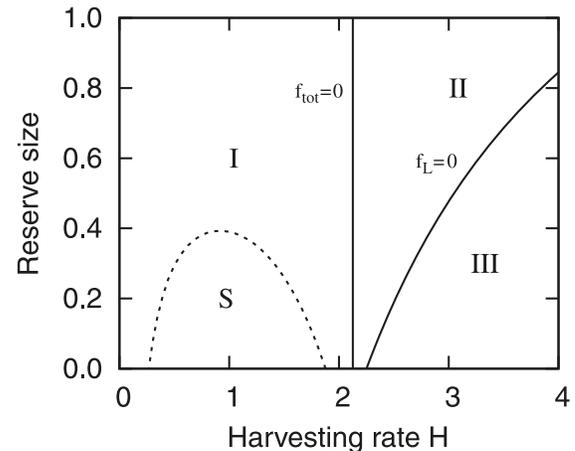

the population reproduction rate with increasing mortality. This response is stronger (at high population density) for net-production allocation than for gross-production allocation, explaining the different results for these two types of models. The logisic MPA model shows that overcompensation is found only when the logistic density dependence affects the birth rate (instead of the death rate). In the size-structured model, the birth rate depends not only on the fecundity (determined by gross-production allocation), but also on the age at maturation and survival to maturation, which are both density-dependent themselves. By consequence, the presence of a juvenile life stage accentuates the density dependence in the birth rate to such an extend that it results in overcompensation, despite gross-production allocation.

With respect to the second factor (larval dispersal), our results stress the need to distinguish between migration of newborns and of older individuals. Whereas the former amounts to a redistribution of biomass production, the latter amounts to a redistribution of biomass standing stock. Our main result depends critically on this distinction; only the redistribution of biomass production can result in the MPA being a sink, because the production can be higher in the harvested area than in the MPA. By contrast, standing biomass is generally higher in the MPA than in the harvested area (Halpern and Warner 2002; Micheli et al. 2004*b*) and therefore is likely to induce spillover into harvested areas. Although the distinction between larval and adult migration is common in MPA models, its implications for the source–sink status of marine reserves has not been identified before.

Here we note that the strictly negative relation between standing (adult) biomass and mortality found for unstructured models (eq. 15) does not necessarily apply to size-structured populations. Size-structured populations can be limited by different demographic processes, depending on which one of them is most affected by intraspecific compe-

rate (and hence the MPA being a larval source), whereas net-production allocation is likely to result in overcompensation (and hence the MPA being a larval sink). However, our complementary analyses of a size-structured model, in which overcompensation is caused by a juvenile growth and maturation despite gross-production allocation, and a logistic model show that the connection between overcompensation and the larval-sink status of MPAs is more general and not limited to net-production models. In other words, overcompensation of the total reproduction rate causes the MPA to be a larval sink, whatever underlying mechanism causes the overcompensation.

Our main result depends on the combination of two factors: (*i*) overcompensation and (*ii*) larval dispersal. When both factors are present, the MPA is predicted to be a larval sink. Our study of three models shows that different mechanisms can underly the first of these factors. Common between all of them is a strong, density-dependent response of

Fig. 8. Steady state of a size-structured model with gross-production allocation. Left panels: fixed size at maturation ($\ell_j = 40$, $\ell_m = 80$). Right panels: absence of juvenile period ($\ell_j < \ell_b$, $\ell_m = 40$). Background mortality (left, $\mu = 0.01$; right, $\mu = 0.1$) and harvesting are size-independent. Top panels: consumer (solid lines) and resource (broken lines) biomass without MPA; adult biomass is represented by the thin solid curve. Middle panels: population birth rate ($\tilde{B}$) without MPA. The left panel displays overcompensation despite gross-production allocation. Bottom panels: predicted biomass flow for corresponding MPA model with $x = 0.3$ and larval dispersal ($\alpha = 1$, $\beta = 0$). Biomass densities (g·m^{-3}) and rates (g·m^{-3}·day^{-1}) are time-averaged over low-amplitude generation cycles (left panels). Parameters and notation are as in de Roos and Persson (2002): $\ell_b = 10$, $\kappa = 0.7$, $I_m = 10^{-4}$, $R_h = 10^{-5}$, $\gamma = 0.006$, $r_m = 0.003$, $\beta = 9 \cdot 10^{-6}$, $\rho = 0.1$, $K = 3$.
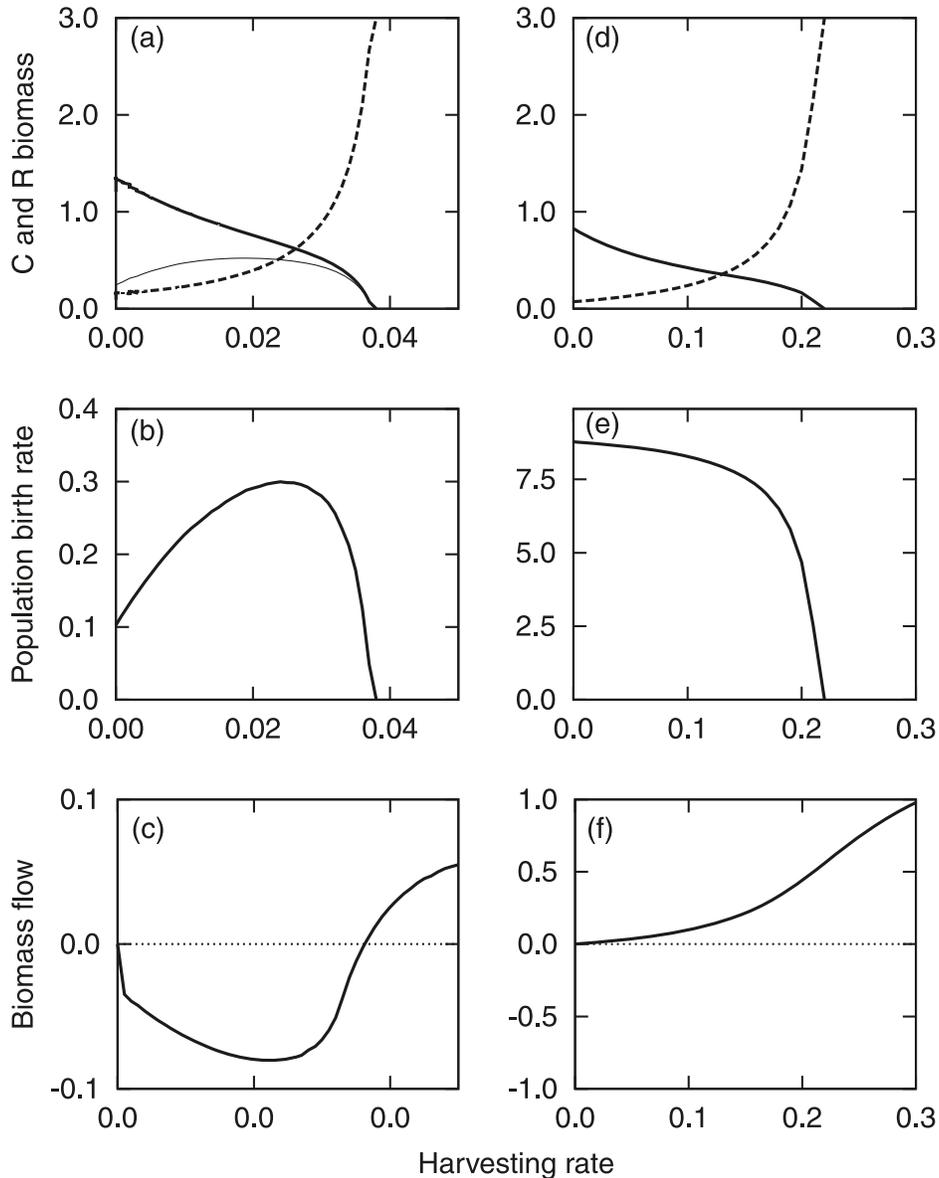
tition (Gurney et al. 1996; de Roos et al. 2007). When a population is regulated by juvenile growth and maturation, then increasing mortality tends to increase the adult standing biomass Although such overcompensation of adult biomass may in turn cause overcompensation of the population reproduction rate, in itself, it may cause a net migration of adults into the MPA. Hence, for maturation-limited populations, we predict that MPAs are likely to be general sinks of biomass, irrespective of the rates of larval and adult migration.

The review of Gerber et al. (2003) shows that previous models have often assumed either migration of larvae only (for example, models assuming LPER) or of adults only.

Our work shows that it is in the case of LPER that overcompensation has the largest potential to cause MPAs to be biomass sinks. This result has not previously been found for the simple reason that the models used do not allow for factors (*i*) and (*ii*) to occur simultaneously. Many models in the literature do not explicitly take into account maintenance costs when computing the birth rate and hence implicitly correspond to the gross-production model (Neubert 2003; Baskett et al. 2006).

For example, the Lotka–Volterra competition models of Baskett et al. (2007) have the potential to display overcompensation, due to their equivalence to the logistic growth

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model (see subsection Logistic MPA model). However, they assume that diffusion migration, i.e., migration of standing stock, results in a flow from high to low density and hence that the MPA is a source. The same is true for the models of Neubert (2003) and Steele and Beet (2003), which are equally based on the logistic growth model. The trophic models of Baskett (2006, 2007) and Baskett et al. (2006, 2007) also assume diffusion migration and hence do not need to distinguish between net- or gross-production allocation. However, we argue that in all of these models, larval flow is likely to be from the MPA to the harvested areas if larval dispersal and, in the trophic model, net-production allocation were assumed.

A second important result of our model is that the relative size of an MPA does not affect the sign of the total biomass flow between the MPA and surrounding areas. How can we understand this? This is a consequence of our assumption of a well-mixed, common dispersal pool. This assumption implies that for each unit of sea surface, the net biomass flow reflects the difference in local production of migrants and the global average production of migrants. Changing the MPA size (x) changes the relative contribution of areas with high and low migrant production and thus influences the average production of migrants. For example, if reserve size x is small and the reserve has a lower migrant production than the fished area, then increasing x will reduce the global average migrant production and hence reduce the influx of migrants into the MPA. Changing x thus has a quantitative effect on steady-state biomass flux (and standing biomass). This is not true, however, for the special case of zero net biomass flow. In this case, each unit of sea surface produces exactly the same amount of migrants. The local production and the global average are hence the same, irrespective of the size of the MPA. Changing the reserve size x has absolutely no effect on biomass flow or on the standing stock biomass.

Increasing reserve size is hence not likely to qualitatively improve the functioning of MPAs (in terms of the source–sink status of the MPA). Figure 7 illustrates that in the range of realistic harvesting rates (i.e., $H \approx 0.2$ to 1), the MPA is a biomass sink for both larvae and adults, no matter the size of the reserve. Only for heavily overexploited fisheries ($H > 2$) does the MPA function as a biomass source.

All of the models that we have discussed are continuous-time models. But what about discrete-time models? Many fisheries models are formulated in discrete time, based on the Ricker or Beverton–Holt models, so the question seems relevant. There is no reason to presume that for discrete-time models, the relation between overcompensation and the source–sink status of MPAs should not hold, in combination with the redistribution of larvae. For example, in the discrete time, predator–prey model of Micheli et al. (2004a), it is assumed that larvae enter a common dispersal pool. We have simulated their model, simplified by excluding the MPA, and found that the steady–state value of the variable L (equivalent to our $\tilde{B}$), increases with fishing mortality for high values of the parameter a. Based on this observation, our results thus predict that in this model, the MPA can be a larval sink. Micheli et al. (2004a) did not, however, compute the direction of the larval flow.

More generally, for discrete-time models, whenever the

recruitment rate displays overcompensation, larval redistribution is expected to result in larval flow from the harvested area to the MPA. This should be the case of models based on the Ricker model, which is the classical example of overcompensation, in contrast to the Beverton–Holt model, which displays undercompensation. However, the actual dynamics will depend on how the density dependence in such models is assumed to depend on the underlying vital rates (birth, death, growth, maturation).

Acknowledgments

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